Journal of General Microbiology (1983), **129**, 1743–1813. *Printed in Great Britain*

Numerical Classification of *Streptomyces* and Related Genera

By S. T. WILLIAMS,[1]* M. GOODFELLOW,[2] G. ALDERSON,[3] E. M. H. WELLINGTON,[4] P. H. A. SNEATH[5] AND M. J. SACKIN[5]

[1]*Department of Botany, University of Liverpool, Liverpool L69 3BX, U.K.*
[2]*Department of Microbiology, University of Newcastle, Newcastle upon Tyne NE1 7RU, U.K.*
[3]*School of Studies in Medical Sciences, University of Bradford, Bradford BD7 1DP, U.K.*
[4]*Department of Biology, Liverpool Polytechnic, Liverpool L3 3AF, U.K.*
[5]*Department of Microbiology, University of Leicester, Leicester LE1 3RH, U.K.*

(*Received 18 June 1982; revised 8 November 1982*)

Four hundred and seventy-five strains, which included 394 type cultures of *Streptomyces* and representatives of 14 other actinomycete genera, were studied. Overall similarities of these strains for 139 unit characters were determined by the S_{SM} and S_J coefficients and clustering by the UPGMA algorithm. Test error and overlap between the phena defined were within acceptable limits. Cluster-groups were defined by the S_{SM} coefficient at the 70·1% similarity (S) level and by the S_J coefficient at the 50% S-level. Clusters were distinguished at the 77·5% S_{SM} and 63% S_J S-levels. Groupings obtained with the two coefficients were generally similar, but there were some changes in the definition and membership of cluster-groups and clusters.

The phenetic data obtained, together with those from previous diverse studies, indicated that the genera *Actinopycnidium*, *Actinosporangium*, *Chainia*, *Elytrosporangium*, *Kitasatoa* and *Microellobosporia* should be reduced to synonyms of *Streptomyces*, while *Intrasporangium*, *Nocardioides* and *Streptoverticillium* remained as distinct genera in the family *Streptomycetaceae*. *Nocardiopsis dassonvillei* also showed strong phenetic affinity to *Streptomyces*, despite its chemotaxonomic differences. *Actinomadura sensu stricto* was phenetically distinguishable from *Streptomyces* and '*Nocardia*' *mediterranea* was recognized as a taxon distinct from both these genera and from *Nocardia sensu stricto*.

Most of the *Streptomyces* type cultures fell into one large cluster-group. At the 77·5% S_{SM} S-level, they were recovered in 19 major and 40 minor clusters, with 18 strains recovered as single member clusters. The status of the latter as species was therefore confirmed. Most of the minor clusters, consisting of two to five strains, can also be regarded as species. The major clusters varied in size (from 6 to 71 strains) and in their homogeneity. Therefore, it is suggested that they be regarded as species-groups until further information is available. The results provide a basis for the reduction of the large number of *Streptomyces* species which have been described. They also demonstrate that the previous use of a limited number of subjectively chosen characters to define species-groups or species has resulted in artificial classifications.

INTRODUCTION

The genus *Streptomyces* was proposed by Waksman & Henrici (1943) for aerobic, spore-forming actinomycetes which had been previously termed *Actinomyces* (Krainsky, 1914; Waksman & Curtis, 1916; Buchanan, 1918; Waksman, 1919, 1940; Lieske, 1921; Ørskov, 1923; Jensen, 1930, 1931; Krasilnikov, 1938; Baldacci, 1939). The genus currently accommodates aerobic Gram-positive actinomycetes that are highly oxidative, form extensive branching substrate and aerial mycelia containing LL-diaminopimelic acid (L-DAP) and glycine but no characteristic sugar in the wall (wall chemotype I *sensu* Lechevalier & Lechevalier, 1970*a*, *b*),

0022-1287/83/0001-0649 $02.00 © 1983 SGM

and have a DNA base composition within the range 69 to 73 mol % guanine (G) plus cytosine (C) (Pridham & Tresner, 1974*a*). Fragmentation of the substrate mycelium is infrequent and spores are rarely produced on the substrate hyphae (Shirling & Gottlieb, 1968*a*, 1976). The aerial hyphae usually bear long chains of spores (>50 spores), but in certain species shorter spore chains occur (Becker *et al.*, 1965; Shirling & Gottlieb, 1968*a*). *Streptomyces* and related genera with a wall chemotype I have recently been shown to form a phylogenetically distinct taxon in 16S rRNA oligonucleotide sequencing and DNA–rRNA studies (Stackebrandt & Woese, 1981; Stackebrandt *et al.*, 1981).

Streptomycetes are well-known as a rich source of antibiotics and proof of the novelty of an antibiotic has frequently rested on the description of the producer as a new species. This practice, coupled with the failure of taxonomists to find reliable tests for the identification of streptomycetes, has resulted in the proliferation of 'species', many of which were proposed on trivial differences in morphological and cultural properties (Waksman, 1957). Between 1940 and 1957 over 1000 *Streptomyces* species were described (Pridham *et al.*, 1958), a number which had swollen to about 3000 by 1970, although many of these additional taxa had merely been cited in the patent literature (Trejo, 1970).

Numerous classifications were devised to accommodate the increasing number of *Streptomyces* species, most of them based on a few subjectively chosen morphological and pigmentation properties which were rarely studied under standardized growth conditions. Gause *et al.* (1957) recognized 15 groups or series distinguished by aerial and substrate mycelium colour, Pridham *et al.* (1958), 42 groups defined by sporophore morphology and aerial mycelium colour, Shinobu (1958), 13 groups based on sporophore morphology, melanin and nitrite production, while Waksman (1961) classified over 250 species into 16 series using aerial and substrate mycelium colour, spore chain morphology, melanin production and a number of other properties including proteolysis. Some taxonomists equated series with species. Pridham *et al.* (1965) reduced 400 *Streptomyces* species to 8 on the basis of spore ornamentation and spore chain morphology. Pridham (1976) recognized 10 species on the same grounds, whereas Hütter (1967) described 41 species using four criteria, sporophore morphology, aerial and substrate mycelium colour and melanin production. Biochemical, nutritional and physiological characters have also been frequently used in streptomycete systematics, but have usually been applied to only selected species (Pridham & Gottlieb, 1948; Okami, 1952; Benedict *et al.*, 1955; Waksman, 1957; Shinobu, 1958; Tresner & Danga, 1958; Flaig & Kutzner, 1960; Gordon, 1966; Williams, 1967; Gordon & Horan, 1968*a*; Nitsch & Kutzner, 1960; 1969*a*, *b*; Tresner *et al.*, 1968; Ziegler & Kutzner, 1973; Kutzner *et al.*, 1978).

By the early 1960s, it was becoming increasingly clear that streptomycete taxonomy had serious problems. In 1964, a collaborative study, the International *Streptomyces* Project (ISP), was established to furnish reliable descriptions of authentic, extant type strains of *Streptomyces* and related taxa using a small number of traditional tests applied under standard conditions (Shirling & Gottlieb, 1966; Gottlieb & Shirling, 1967). Over 450 species were redescribed, and type and neotype strains were deposited in four recognized culture collections (Shirling & Gottlieb, 1968*a*, *b*, 1969, 1972). However, attempts to compare and delineate *Streptomyces* species were considered to be beyond the scope of the project. Despite the limitations of the ISP, especially its narrow data base, the results were used by several workers to construct identification schemes (Arai & Mikami, 1969; Küster, 1972; Nonomura, 1974; Szabo *et al.*, 1975), some of which involved computer analysis (Gyllenberg, 1970, 1974, 1976; Gyllenberg *et al.*, 1975).

Taxometric studies using a wider range of characteristics were first applied to the genus *Streptomyces* and some related taxa by Silvestri and his colleagues (Gilardi *et al.*, 1960; Hill *et al.*, 1961; Silvestri *et al.*, 1962). In the most extensive report (Silvestri *et al.*, 1962), streptomycetes were assigned to 25 centres of variation, the major groups clustering around *Streptomyces lavendulae* (Group A, 33 strains), *S. violaceoruber* (Group B, 46 strains), *S. griseus* (Group C, 37 strains), *S. flavus* (Group D, 24 strains) and *S. fradiae* (Group F, 18 strains). The unsatisfactory state of streptomycete taxonomy was indicated by the frequency with which strains bearing the same name occurred in different groups; for instance, organisms labelled *S. violaceus* were

recovered in three separate major phena. On the other hand, Sphere II of Group A contained several strains of the section *Biverticillus* of Pridham *et al.* (1958). Group C included strains such as *S. microflavus* CBS, ETH 10206, *S. odorifer* ISP 5347 and *S. praecox* ISP 5393, which were placed in the 'griseus' group by Ettlinger *et al.* (1958), as well as a number of species subsequently reduced to synonyms of *S. griseus* (Gordon & Horan, 1968*a*). Gyllenberg *et al.* (1967), in comparing factor analysis with the earlier numerical taxonomy of Wóznicka (1965, 1967), recovered streptomycetes of the 'yellow' series in five clusters, but emphasized that the classification rested on a small number of strains and an inadequate sample of tests. Though very few of these strains were studied by Silvestri *et al.* (1962), it was again evident that streptomycetes fell into relatively few major clusters compared to the many species names borne by the strains. Silvestri and his co-workers did not propose any nomenclatural revision, though a probabilistic key was constructed for the identification of streptomycetes (Hill & Silvestri, 1962; Möller, 1962). A number of other studies using a variety of statistical analyses indicated that the genus *Streptomyces* was overclassified (Kurylowicz *et al.*, 1969, 1970, 1975, 1976; Gyllenberg, 1970; Paszkiewicz, 1972; Szulga, 1978), while in a limited study, Williams *et al.* (1968) confirmed the naturalness of certain colour groupings. There is also some preliminary evidence that acidophilic and neutrophilic streptomycetes fall into different clusters (Williams & Khan, 1974; Khan & Williams, 1975).

The genus *Streptomyces* is classified in the family *Streptomycetaceae* (Waksman & Henrici, 1943), which also includes a number of taxa that were initially morphological in concept. Thus, strains of *Chainia* typically form sclerotia (Thirumalachar, 1955); *Streptoverticillium* bears verticils at regular intervals (Baldacci, 1958); *Actinosporangium* produces sporangia (Krasilnikov & Yuan, 1961), *Actinopycnidium*, pycnidia (Krasilnikov, 1962), *Microellobosporia*, sporangia on short sporophores (Cross *et al.*, 1963; Rancourt & Lechevalier, 1963), *Elytrosporangium*, pod-shaped vesicles on the substrate mycelium (Falcao de Morais *et al.*, 1966), and *Kitasatoa*, club-shaped vesicles at the tips of the substrate and aerial hyphae (Matsumae & Hata, 1968). The status and relationships of these taxa both to one another and to the genus *Streptomyces* is not clear (Baldacci, 1958; Waksman, 1961; Küster, 1963; Becker *et al.*, 1965; Hütter, 1965, 1967, 1970; Lechevalier & Lechevalier, 1965, 1967, 1970*b*; Baldacci & Locci, 1966; Baldacci *et al.*, 1966; Falcao de Morais, 1967; Prauser *et al.*, 1967; Prauser, 1970, 1978; Cross & Goodfellow, 1973; Lechevalier *et al.*, 1973; Prauser & Bergholz, 1974; Kutzner, 1981). *Intrasporangium* (Kalakoutskii *et al.*, 1967), *Sporichthya* (Lechevalier *et al.*, 1968) and *Nocardioides* (Prauser, 1976*a*) are morphologically distinct from *Streptomyces* and have been assigned to the family *Streptomycetaceae* primarily on the basis of wall chemotype.

In the current edition of *Bergey's Manual of Determinative Bacteriology* (Pridham & Tresner, 1974*b*), the classification of the genus *Streptomyces*, which includes species previously assigned to *Chainia*, is based upon ISP data. Thus, 463 species are classified into 43 groups based on micromorphology and pigmentation; the groups are subdivided by carbon utilization patterns. The genera *Microellobosporia*, *Sporichthya* and *Streptoverticillium* are recognized; *Actinopycnidium*, *Actinosporangium* and *Intrasporangium* are listed as genera *incertae sedis* (Pridham & Tresner, 1974*a*), while *Kitasatoa* is classified in the family *Actinoplanaceae* (Couch & Bland, 1974). The genus *Microtetraspora* (Thiemann *et al.*, 1968), which produces four spores at the end of short sporophores and contains *meso*-DAP with traces of the L-isomer but no characteristic sugars in the wall (chemotype III *sensu* Lechevalier & Lechevalier, 1970*a*, *b*), is also listed as a genus *incertae sedis* in the family *Streptomycetaceae*. All of the genera mentioned above are cited in the *Approved Lists of Bacterial Names* (Skerman *et al.*, 1980), as are 336 species of *Streptomyces*.

The aim of the present study was to determine the intra- and suprageneric relationships of *Streptomyces*. Strains studied included 394 type cultures of *Streptomyces* described in the ISP project, marker cultures of *Actinomadura*, *Actinopycnidium*, *Actinosporangium*, *Chainia*, *Elytrosporangium*, *Intrasporangium*, *Kitasatoa*, *Microellobosporia*, *Microtetraspora*, *Nocardia*, *Nocardioides*, *Nocardiopsis*, *Saccharopolyspora*, *Streptoverticillium*, together with streptomycetes from soil and isolates from fodder and hay (Goodfellow *et al.*, 1979). These were compared using numerical phenetic techniques.

METHODS

Strains. 475 test strains representing 15 genera were obtained from both public and private culture collections (Table 1); 44 duplicate cultures were also included. Binomials in inverted commas are not on the *Approved Lists of Bacterial Names* (Skerman *et al.*, 1980) and have not been validly published since 1 January 1980. Genus names in inverted commas indicate that the generic status of the strain is still uncertain. Where possible, type cultures were included. Detailed strain histories of the 394 ISP cultures examined can be found elsewhere (Shirling & Gottlieb, 1968*a*, *b*, 1969, 1972). All strains were stored on yeast/malt extract agar slopes (Pridham *et al.*, 1956–1957) both at room temperature and at −25 °C, on slopes of modified Bennett's agar (MBA) (Jones, 1949) with glucose replaced by glycerol, at 4 °C. Suspensions of spores or mycelial fragments were stored in glycerol (20%, v/v) at −20 °C (Wellington & Williams, 1978).

Inoculation and incubation. Each strain was examined for 162 unit characters. Thawed glycerol suspensions served as inocula for all but the sole carbon source utilization tests, where 7- to 10-d-old cultures grown on MBA were used. All tests were carried out at least once on each strain, being repeated where ambiguous or clearly unexpected results were obtained. Inoculated media were usually incubated at 25 °C, but thermophiles, '*Streptomyces thermoflavus*' ISP 5574, *Streptomyces thermonitrificans* ISP 5579 and *Streptomyces thermovulgaris* ISP 5444, were incubated at 45 °C. Strains were grown on media at a pH close to 7·0, except for the acidophilic soil isolates (H1, MR2, MR10, MR19, MR22, SW1, SW5 and SW10) which were grown on media adjusted to pH 5·5 with sterile 1 M-HCl. Morphological, pigmentation, antimicrobial activity, degradation and antibiotic-sensitivity tests were carried out in Petri dishes, as were the enzymic tests, apart from nitrate reduction, hydrogen sulphide production, hippurate hydrolysis, and aesculin, allantoin, arbutin and urea degradation, all of which were performed in test tubes. Melanin production, growth and nutritional tests were studied in polystyrene Repli dishes (Sneath & Stevens, 1967). Incubation times for specific tests are given below.

Morphology and pigmentation. Spore chain morphology was examined by light and scanning electron microscopy (SEM) (Williams & Davies, 1967) of 14-d-old cultures on inorganic salts/starch agar (ISP medium 4; Difco). The morphological categories proposed by Pridham *et al.* (1958) were employed using the section terminology of the ISP (Shirling & Gottlieb, 1968*a*). Where two spore chain sections were observed on a culture, both were recorded. Spore surface ornaments were determined on SEM preparations. Growth on coverslips was fixed in formaldehyde vapour for 24 h. Ornaments were assigned to the categories of Tresner *et al.* (1961) or to the 'rugose' section of Dietz & Matthews (1971). Light and SEM preparations were also examined for the presence of sclerotia, substrate spores and fragmentation of the substrate mycelium.

Aerial spore-mass colour was determined on the cultures used for morphological examination. Colours were matched to one of the seven colour wheels of Tresner & Backus (1963) using the methods of Shirling & Gottlieb (1966). Substrate mycelial pigments were observed after 14 d (3 d at 45 °C for thermophiles) on ISP medium 4 (Shirling & Gottlieb, 1966). The production of soluble pigments was determined on glycerol/asparagine agar (ISP medium 5; Difco) after 14 d (3 d at 45 °C for thermophiles); pigments were categorized into one of five colour groups (Table 3). The pH sensitivity of substrate and soluble pigments was also determined (Shirling & Gottlieb, 1966). All of the colour determinations were made in a box under standard lighting of illuminant C (fluorescent batten; Thorn Electricals, Thorn House, London, U.K.), which approximates to average daylight. Melanin production was determined on ISP media 6 and 7 (Difco) after 4 d for mesophiles and 3 d at 45 °C for thermophiles (Shirling & Gottlieb, 1966).

Antimicrobial activity. The ability to inhibit the growth of eight test organisms (Table 3) was observed using an overlay technique. Spot-inoculated colonies on nutrient agar plates (Oxoid CM3) were inverted over 1·5 ml chloroform (BDH) for 40 min. Killed colonies were then overlaid with 5 ml sloppy agar (0·7%, w/v, Oxoid nutrient agar no. 2) inoculated with the test organisms. Zones of inhibition were measured after 24 h at 30 °C.

Biochemical tests. Activity on egg-yolk medium (EY) was examined by the method of Nitsch & Kutzner (1969*b*). Precipitate development was clearest on a modified EY medium containing: bacteriological peptone (Oxoid), 1·0% (w/v); glucose, 0·1%; NaCl, 1·0%; yeast extract (Oxoid), 0·5%; Bacto-agar (Difco), 1·2%; egg-yolk emulsion (Oxoid), 5·0% (v/v); pH 7·0. Proteolysis was scored after 2 d, lecithinase and lipolysis at 2, 4 and 6 d (1, 2 and 4 d at 45 °C for thermophiles). Pectinolytic activity was determined according to Hankin *et al.* (1971) using a modified medium made up in three parts containing: (*a*) KH_2PO_4, 0·4% (w/v); Na_2HPO_4, 0·6%; (*b*) pectin (from citrus fruit rind; Koch-Light), 0·5%; and (*c*) $(NH_4)_2SO_4$, 0·2%; yeast extract (Oxoid), 0·1%; $MgSO_4.7H_2O$, 0·2%; $FeSO_4.7H_2O$, 0·0001%; $CaCl_2$, 0·0001%; Bacto-agar (Difco), 1·0%; pH 7·4. Hydrolysis zones were detected after 4 and 6 d (2 and 4 d at 45 °C for thermophiles) by flooding plates with an aqueous solution of hexadecyltrimethylammonium bromide (1%, w/v). Catalase production was detected by adding a few drops of 20 volume H_2O_2 on to 7-d-old colonies grown on MBA; evolution of oxygen was detected under a binocular microscope. Nitrate reduction was determined after 7 and 14 d (4 and 6 d at 45 °C for thermophiles) by addition of 0·2 ml each of Griess–Ilosvay reagents I and II to stab cultures in a sloppy nitrate medium (NM) composed of nutrient broth (Oxoid CM1) supplemented with KNO_3 (0·2%, w/v) and Bacto-agar (0·6%; Difco). Hydrogen sulphide formation was detected by inserting sterile lead acetate filter paper strips (Küster & Williams, 1964) into the necks of NM tubes and examining for blackening after the same incubation periods. Hippurate agar (Ziegler & Kutzner, 1973)

modified from Thirsk (1957) was used to detect hydrolysis after 6, 12 and 18 d (4 and 6 d at 45 °C for thermophiles). β-Lactamase production was determined according to O'Callaghan *et al.* (1972) on 4 d cultures grown on yeast/peptone plus glycerol medium (YPG) comprising: yeast extract (Oxoid), 0·3% (w/v); peptone (Oxoid), 0·06%; glycerol, 1·0% (w/v); agar (Oxoid no. 1), 1·2%; pH 6·5 and on Beecham's FS medium which contained: soya peptone (Lab M), 1·0% (w/v); glucose, 2·0%; $CaCl_2$, 0·0001%; $CaCO_3$, 0·02%; Na_2SO_4 (anhydrous), 0·1%; agar (Oxoid no. 1), 1·2%; pH 7·4. The production of β-lactamase inhibitor was determined on Beecham's FS agar and YPG agar; inhibitors were detected by the addition of approximately 10 units of *Klebsiella aerogenes* K1 β-lactamase to the agar overlay, zones of inactivity being observed according to O'Callaghan *et al.* (1972).

Degradative tests. The degradation of adenine, tyrosine (0·5%, w/v), hypoxanthine, xanthine, xylan (0·4%, w/v), elastin, keratin (0·3%, w/v), casein (1%, w/v, skimmed milk), guanine (0·05%, w/v) and testosterone (0·1%, w/v) was detected in MBA after 7, 14 and 21 d (3 and 7 d at 45 °C for thermophiles); clearing of the insoluble compounds from under and around areas of growth was scored as positive. Gelatin (0·4%, w/v) and starch (1·0%, w/v) degradation were detected in the same basal medium after 7 d (3 d at 45 °C for thermophiles) by flooding plates with acidified $MgCl_2$ solution (Frazier, 1926) and iodine solution (Cowan, 1974), respectively, and scoring zones of clearing as positive. The degradation of DNA (0·2%, w/v) and RNA (0·3%, w/v) was observed using Bacto DNase Test agar (Difco) and tryptone agar (Goodfellow *et al.*, 1979), respectively; in each case 7 d plates (3 d at 45 °C for thermophiles) were flooded with 1 M-HCl and clearance zones were recorded as positive. Sierra's (1957) medium supplemented with Tweens 20, 40, 60 and 80 (1%, v/v) was examined for opacity after 3, 7 and 14 d (1, 3 and 7 d at 45 °C for thermophiles). Chitinolytic activity was observed after 14, 21 and 28 d (4 and 8 d at 45 °C for thermophiles) by the appearance of zones of clearing in colloidal chitin agar (Hsu & Lockwood, 1975); only zones of >4·5 mm were scored as positive because weak positive reactions were not reproducible. The degradation of allantoin and urea was recorded after 7, 14, 21 and 28 d (3, 7 and 14 d at 45 °C for thermophiles) using the media and methods of Gordon (1966, 1968), while the breakdown of tributyrin (Oxoid) was observed after 7 and 14 d (3 and 17 d at 45 °C for thermophiles). Aesculin (0·1%, w/v) and arbutin (0·1%, w/v) were determined by the method of Kutzner (1976) using a modified medium containing yeast extract (Oxoid), 0·3% (w/v); ferric ammonium citrate, 0·05% and Lab M agar, 0·75%. Tubes were examined after 7, 14 and 21 d (3 and 7 d at 45 °C for thermophiles); any slight production of melanin was detected in the negative control. Blackening of the test media indicated a positive result.

Antibiotic resistance. Strains were tested for their ability to grow in the presence of 11 antibiotics, using the freeze-dried filter paper disc method of Goodfellow & Orchard (1974). Discs previously soaked in cephaloridine (Glaxo; 100 μg ml^{-1}), dimethychlortetracycline hydrochloride (Cyanamid; 500 μg ml^{-1}), gentamicin sulphate (Roussel; 100 μg ml^{-1}), lincomycin hydrochloride (Upjohn; 100 μg ml^{-1}), neomycin sulphate (Biorex; 50 μg ml^{-1}), penicillin G (Oxoid; 10 i.u. ml^{-1}), rifampicin (Lepetit; 50 μg ml^{-1}), streptomycin sulphate (Glaxo; 100 μg ml^{-1}), tobramycin (Lilly; 50 μg ml^{-1}), triacyl oleandomycin (Pfizer; 100 μg ml^{-1}) and vancomycin hydrochloride (Lilly; 50 μg ml^{-1}) were placed on MBA which had been inoculated with 0·1 ml of a glycerol spore suspension. Readings were taken at 1, 2, 3 and 7 d for all strains and resistance was scored as a positive result; the first readable result was scored for computation.

Growth tests. Tolerance to temperature, pH and chemical inhibitors was tested using MBA. Growth at 25, 37 and 45 °C was read after 7 and 14 d, that at 4 and 10 °C after 6 weeks, and growth at pH 4·3 and pH 7·3 was read after 7 and 14 d (3 and 7 d at 45 °C for thermophiles). Resistance to a range of chemical inhibitors (Table 3) was scored after 7 and 14 d (3 and 7 d at 45 °C for thermophiles); in all cases growth was scored as positive.

Organic compounds as sole source of carbon. The ability of strains to use 25 different sole carbon sources (Table 3) was examined on carbon utilization agar (ISP medium 9; Difco), as recommended by Shirling & Gottlieb (1966). Carbon sources were added at 1·0% (w/v) with the exception of sodium acetate, citrate, malonate, propionate and pyruvate, which were used at 0·1% (w/v). Growth was scored after 7, 14 and 21 d (3, 7 and 14 d at 45 °C for thermophiles). In the case of the actinomaduras the basal medium was supplemented with vitamin B_1 (0·005%, w/v).

Compounds as sole source of nitrogen. Strains were tested for their ability to use 11 nitrogen sources (0·1%, w/v) in a basal medium consisting of: D-glucose, 1·0% (w/v); $MgSO_4 . 7H_2O$, 0·05%; NaCl, 0·05%; $FeSO_4 . 7H_2O$, 0·001%; K_2HPO_4, 0·1%; Bacto-agar (Difco), 1·2%; pH 7·4. Growth was scored after 15 d (6 d at 45 °C for thermophiles) by comparing test plates with both negative and positive controls, the latter consisting of the basal media supplemented with either L-asparagine or L-proline.

Coding of data. Nearly all of the characters existed in one of two mutually exclusive states and were scored plus (1) or minus (0). Qualitative multistate characters, such as pigmentation and spore chain morphology, were coded as several independent characters and each was scored plus (1) for the character state shown and minus (0) for the alternative. Quantitative multistate characters, such as tolerance to chemical inhibitors, were coded using the additive method of Sneath & Sokal (1973). Twenty-three characters were deleted from the data matrix because they showed little or no separation value, or were poorly reproducible. The final $n \times t$ table, therefore, contained data for 475 bacteria (t) and 139 unit characters (n) (Table 3). The binary data were recorded on standard IBM punch cards.

Computer analysis. Data were examined using the Clustan 1C program (Wishart, 1978) on an IBM 370/180

computer using both the simple matching coefficient (S_{SM}; Sokal & Michener, 1958), which includes both positive and negative matches, and the Jaccard coefficient (S_J; Sneath, 1957) including positive matches only. Clustering was achieved using the unweighted average linkage (UPGMA) algorithm (Sneath & Sokal, 1973) and results are presented as dendrograms. The data were also examined on an ICL 1906A computer using TAXPAK (M. J. Sackin, unpublished), which included the IGROUPS program providing character value statistics on specified clusters of strains.

The distinctiveness of major clusters was examined using a significance test derived for testing dichotomous clusters in a dendrogram on the assumption that clusters are approximately multivariate normal (Sneath, 1977). The method was based on an index of disjunction, W, that corresponded to a degree of overlap V_G. The significance test consisted in determining whether the observed overlap was significantly less than an expected overlap. This was done by determining whether a t statistic derived from the observed overlap exceeded a non-central t value for the expected degree of overlap. Overlap statistics were calculated between all pairs of major clusters using the OVCLUST program (Sneath, 1979) and intercentroid distances and standard deviations along the intercentroid (q) axis were obtained from the IGROUPS program. OVCLUST was modified to perform automatically on all pairs of clusters using cards output by IGROUPS and was run on a CDC CYBER 73 computer. The chosen critical value of overlap, V_O, was set at 5%. This value was chosen because it is somewhat less than the expected overlap for continuous clusters (Sneath, 1977).

Test reproducibility. The test results for the 44 duplicate cultures and their partners (Table 2) were compared for all 139 unit characters and an estimate of test variance (s_i^2) calculated (formula 15; Sneath & Jackson, 1972). The average test variance was determined to obtain a pooled variance (s^2), which was used to calculate the average probability (p) of an erroneous test result (formula 4; Sneath & Johnson, 1972). The similarity between duplicates was estimated by computation of the S_{SM} coefficient. A further calculation of S_{SM} values was made using TAXPAX with missing and inapplicable scores coded NC (non-comparable; Sneath & Sokal, 1973).

RESULTS

Test error and final data matrix

Inclusion of duplicate strains in the analysis enabled experimental test error to be calculated (Table 2). The average probability (p) or an erroneous test result was 3·36%, calculated from the pooled variance ($s^2 = 0{\cdot}0325$) of all the unit characters scored for the duplicate cultures. The 44 pairs of identical strains showed a mean observed similarity of 93·1% $S_{SM} \pm 0{\cdot}35$ (mean value ± S.E.) when the test data were coded 0 or 1. The use of the NC code instead of 0 for inapplicable and missing scores gave an average similarity of 93·0% $S_{SM} \pm 0{\cdot}35$. It can be seen from Table 2 that the majority of the tests or groups of tests showed s_i^2 values below 0·05. The reproducibility of qualitative multistate characters was determined by estimation of s_i^2 values for each character state coded as a unit character. In such instances the s_i^2 value is a slight underestimate, as the character states are mutually exclusive and negative matches increase the percentage agreement between duplicates. The results for tolerance towards phenylethanol (0·2%, v/v) and growth on KNO_3 (0·05%, w/v), L-cystine, L-leucine, L-isoleucine, L-lysine and L-tryptophan (0·1%, w/v) as sole nitrogen sources showed test variance greater than 0·1 and were consequently excluded from the data matrix.

The results of a further 16 tests were deleted from the data matrix as they showed little or no separation value. Thus, all strains were catalase-positive, degraded tributyrin and Tweens 20, 40 and 60, used glucose (1·0%, w/v) as sole carbon source, grew in the presence of crystal violet (0·00001%, w/v) and phenol (0·01%, w/v), were inhibited by potassium tellurite (0·1%, w/v) and mainly failed to use KNO_2 (0·3%, w/v), creatine or taurine (0·1%, w/v) as sole nitrogen sources. Most of the strains grew at 25 °C and used L-asparagine and L-proline (0·1%, w/v) as sole source of nitrogen. The results from the carboxymethylcellulose test were also excluded from the numerical analyses as positive reactions were difficult to read and unreproducible. The final data matrix, therefore, contained 475 strains and 44 duplicate cultures against 139 unit characters.

Clustering of strains using the S_{SM} coefficient with the UPGMA algorithm

Composition and characterization of cluster-groups. The classification based on the S_{SM}/UPGMA analysis is described in detail as it gave the most compact clusters. Cluster-groups

Table 1. *Designation and source of cultures assigned to cluster groups (defined at 70·1% S_{SM}/UPGMA) and clusters (defined at 77·5% S_{SM}/UPGMA)*

Binomials in inverted commas are not on the *Approved Lists of Bacterial Names* (Skerman *et al.*, 1980) and have not been validly published since 1 January 1980. Genus names in inverted commas indicate that the generic status of the strain is still uncertain.

Cluster-group A

Strains assigned to cluster 1 (*Streptomyces albidoflavus*)

Subcluster 1A

ISP 5445	*Streptomyces albidoflavus*	A. Seino; KCC S-0446. ATCC 25422
ISP 5001	*S. canescens*	H. J. Kutzner; DSM 40001. ATCC 19736
ISP 5364	'*S. citreus*'	A. Seino; KCC S-0464. ATCC 25441
ISP 5233	*S. coelicolor*	A. Seino; KCC S-0065. ATCC 23899
ISP 5485	'*S. coriofaciens*'	A. Seino; KCC S-0741. ATCC 14155
ISP 5296	'*S. craterifer*'	T. Cross, CUB 302. ATCC 25445
ISP 5130	*S. felleus*	A. Seino; KCC S-0368. ATCC 19752
ISP 5324	*S. gougerotii*	A. Seino; KCC S-0478. ATCC 10975
ISP 5372	*S. intermedius*	A. Seino; KCC S-0483. ATCC 3329
ISP 5321	'*S. krainskii*'	A. Seino; KCC S-0487. ATCC 25465
ISP 5131	*S. limosus*	H. J. Kutzner; DSM 40131. ATCC 19778
*ISP 5347	*S. odorifer*	A. Seino; KCC S-0803. ATCC 6246
ISP 5077	*S. rutgersensis*	H. J. Kutzner; DSM 40077. ATCC 3350
ISP 5394	*S. sampsonii*	A. Seino; KCC S-0515. ATCC 25495
ISP 5537	'*S. saprophyticus*'	A. Seino; KCC S-0827. ATCC 3351
ISP 5585	'*S. tetanusemus*'	A. Seino; KCC S-0839. ATCC 27471
135, 442, 464, 195	*Streptomyces* spp.	S. T. Williams; LIV 135; LIV 422; LIV 464; LIV 195

Subcluster 1B

ISP 5320	'*Streptomyces albidus*'	S. T. Williams; A45. ATCC 25423
*ISP 5043	*S. alboniger*	A. Seino; KCC S-0563. ATCC 12461
ISP 5136	*S. albovinaceus*	R. Locci; IPV 1611. ATCC 15823
ISP 5326	*S. alboviridis*	A. Seino; KCC S-0449. ATCC 25425
ISP 5361	*S. anulatus*	A. Seino; KCC S-0721.† ATCC 27416
ISP 5055	'*S. aureus*'	T. Cross; CUB 110†
ISP 5417	'*S. aurigineus*'	W. Kuryłowicz; The State Institute of Hygiene, Warsaw, Poland; ATCC 19827
ISP 5232	*S. baarnensis*	R. Locci; IPV 1785. ATCC 23885.
ISP 5598	'*S. bacillans*'	S. T. Williams; A179. ATCC 15855.
ISP 5235	*S. bikiniensis*	W. Kuryłowicz; IMRU 3514†
ISP 5300	*S. cavourensis*	A. Seino; KCC S-0555. ATCC 14889
ISP 5128	*S. chrysomallus*	H. J. Kutzner; DSM 40128.† ATCC 23209
ISP 5265	*S. citreofluorescens*	I. J. Bousfield; NCIB 9806; ATCC 15858
ISP 5147	*S. cremeus*	I. J. Bousfield; NCIB 10030. ATCC 19897
ISP 5148	*S. cyaneofuscatus*	H. J. Kutzner; DSM 40148. ATCC 23619
ISP 5322	*S. fimicarius*	S. T. Williams; A17. ATCC 25449
ISP 5203	*S. fluorescens*	I. J. Bousfield; NCIB 9851. ATCC 15860
ISP 5199	*S. globisporus*	I. J. Bousfield; NCIB 9796. ATCC 15864
ISP 5047	*S. griseinus*	A. Seino; KCC S-0379. ATCC 23915
ISP 5066	*S. griseobrunneus*	H. J. Kutzner; DSM 40066. ATCC 19762
ISP 5236	*S. griseus*	H. J. Kutzner; DSM 40236. ATCC 23345
ISP 5070	*S. lipmannii*	S. T. Williams; A6. ATCC 3331
ISP 5600	'*S. luteolutescens*'	A. Seino; KCC S-0787. ATCC 27445
ISP 5088	*S. niveus*	I. J. Bousfield; NICB 9219. ATCC 19793
ISP 5589	'*S. oligocarbophilus*'	A. Seino; KCC S-0804. ATCC 27453
ISP 5307	'*S. ornatus*'	A. Seino; KCC S-0502. ATCC 23265
ISP 5348	*S. parvus*	S. T. Williams; A83. ATCC 12433
ISP 5019	*S. pluricolorescens*	I. J. Bousfield; NCIB 9813. ATCC 19798
ISP 5395	*S. setonii*	S. T. Williams; A48. ATCC 25497
ISP 5255	*S. sindenensis*	A. Seino; KCC S-0669. ATCC 23963
ISP 5292	*S. spheroides*	S. T. Williams; A116. ATCC 23965
ISP 5459	*S. willmorei*	A. Seino; KCC S-0861. ATCC 6867
253, 463, 595	*Streptomyces* spp.	S. T. Williams; LIV 253; LIV 463; LIV 595
C1, M2, T5	*Streptomyces* spp.	S. T. Williams; C1, M2, T5; soil isolates

Table 1 (*continued*)

	Subcluster 1C	
ISP 5517	*Streptomyces erythraeus*	A. Seino; KCC S-0748. ATCC 11635
ISP 5323	*S. flavogriseus*	A. Seino; KCC S-0475. ATCC 25452
ISP 5062	*S. flavovirens*	H. J. Kutzner; DSM 40062. ATCC 3320
ISP 5067	*S. griseolus*	S. T. Williams; A8. ATCC 3325
ISP 5068	*S. halstedii*	I. J. Bousfield; NCIB 9839. ATCC 10897
ISP 5602	'*S. humifer*'	A. Seino; KCC S-0770. ATCC 13748
*ISP 5508	'*S. naraensis*'	A. Seino; KCC S-0794. ATCC 13788
ISP 5071	*S. nigrifaciens*	H. J. Kutzner; DSM 40071. ATCC 19791
ISP 5023	*S. nitrosporeus*	H. J. Kutzner; DSM 40023. ATCC 12769
ISP 5072	*S. olivaceus*	H. J. Kutzner; DSM 40072. ATCC 3335
ISP 5573	*S. thermodiastaticus*	A. Seino; KCC S-0840. ATCC 27472
049, 039	*Streptomyces* spp.	S. T. Williams; LIV 049; LIV 039
	Strains assigned to cluster 2 ('*Streptoverticillium*' *olivoverticillatum*)	
ISP 5033	*Streptomyces aburaviensis*	A. Seino; KCC S-0613. ATCC 23869
ISP 5123	*S. herbaricolor*	S. T. Williams; A118. ATCC 23922
ISP 5250	'*Streptoverticillium*' *olivoverticillatum*	A. Seino; KCC S-0100. ATCC 25480
	Strain assigned to cluster 3 (*Streptomyces atroolivaceus*)	
ISP 5137	*Streptomyces atroolivaceus*	R. Locci; IPV 1612. ATCC 19725
ISP 5386	*S. aureocirculatus*	A. Seino; KCC S-0454. ATCC 19823
ISP 5141	'*S. candidus*'	H. J. Kutzner; DSM 40141. ATCC 19891
ISP 5561	'*S. cretaceus*'	W. Kuryłowicz; ATCC 3005
*ISP 5210	'*S. fulvoviridis*'	I. J. Bousfield; NCIB 9804. ATCC 15863
G7	*S. olivaceus*	L. J. Nisbet; Glaxo C2118.† ATCC 3126
ISP 5211	*S. olivovidiris*	A. Seino; KCC S-0658. ATCC 15882
ISP 5078	'*S. scabies*'	A. Seino; KCC S-0417. ATCC 23962
ISP 5454	'*S. viridogenes*'	A. Seino; KCC S-0858. ATCC 3372
	Strains assigned to cluster 4 (*Nocardiopsis dassonvillei*)	
A14, A15	*Nocardiopsis dassonvillei*	NCTC 10488; NCTC 10489
	Strains assigned to cluster 5 (*Streptomyces exfoliatus*)	
ISP 5012	*Streptomyces cinereoruber*	I. J. Bousfield; NCIB 9836. ATCC 19740
ISP 5060	*S. exfoliatus*	H. J. Kutzner; DSM 40060. ATCC 12627
ISP 5022	*S. filamentosus*	H. J. Kutzner; DSM 40022. ATCC 19753
ISP 5541	'*S. flavochromogenes*'	A. Seino; KCC S-0752. ATCC 14841
ISP 5064	*S. gardneri*	A. Seino; KCC S-0375. ATCC 23911
ISP 5586	*S. hydrogenans*	A. Seino; KCC S-0771. ATCC 19631
ISP 5164	*S. litmocidini*	H. J. Kutzner; DSM 40164. ATCC 19914
ISP 5016	*S. narbonensis*	H. J. Kutzner; DSM 40016. ATCC 19790
ISP 5314	*S. nashvillensis*	A. Seino; KCC S-0498. ATCC 25476
ISP 5552	*S. omiyaensis*	A. Seino; KCC S-0806. ATCC 27454
ISP 5174	*S. roseolus*	H. J. Kutzner; DSM 40174. ATCC 23210
ISP 5122	*S. roseosporus*	A. Seino; KCC S-0412. ATCC 23958
ISP 5175	*S. roseoviridis*	A. Seino; KCC S-0414. ATCC 23959
ISP 5329	*S. termitum*	I. J. Bousfield; NCIB 9980. ATCC 25499
ISP 5278	*S. umbrinus*	A. Seino; KCC S-521. ATCC 19929
ISP 5279	*S. violaceorectus*	W. Kuryłowicz; ATCC 25514
*ISP 5196	*S. zaomyceticus*	A. Seino; KCC S-0864. ATCC 27482
T1	*Streptomyces* sp.	S. T. Williams; T1, soil isolate
	Strains assigned to cluster 6 (*Streptomyces violaceus*)	
ISP 5189	*Streptomyces cellostaticus*	S. T. Williams; A103. ATCC 23894
ISP 5015	*S. michiganensis*	H. J. Kutzner; DSM 40015. ATCC 14970
ISP 5504	*S. showdoensis*	A. Seino; KCC S-0830. ATCC 15105
ISP 5036	*S. spiroverticillatus*	H. J. Kutzner; DSM 40036. ATCC 19811
ISP 5230	*S. venezuelae*	A. Seino; KCC S-0526. ATCC 10712
ISP 5515	*S. vinaceus*	A. Seino; KCC S-0849. ATCC 27476
ISP 5082	*S. violaceus*	I. J. Bousfield; NCIB 9820. ATCC 15888
ISP 5183	*S. violascens*	W. Kuryłowicz; ATCC 23968

Table 1 (*continued*)

	Strains assigned to cluster 7 ('*Streptomyces roseus*')	
G5	'*Streptomyces lactamdurans*'	L. J. Nisbet; Glaxo C2060
G6	*S. lipmanii*	L. J. Nisbet; Glaxo C1940†
ISP 5076	'*S. roseus*'	H. J. Kutzner; DSM 40076. ATCC 19808
	Strains assigned to cluster 8 ('*Streptomyces alni*')	
ISP 5557	'*Streptomyces alni*'	A. Seino; KCC S-0719. ATCC 27415
M 673	'*Kitasatoa antimyceticus*'	A. Matsumae; KI-104074
	Strains assigned to cluster 9 (*Streptomyces californicus*)	
ISP 5058	*Streptomyces californicus*	S. T. Williams; A43. ATCC 3312
ISP 5125	*S. phaeopurpureus*	W. Kuryłowicz; ATCC 23946
ISP 5983	*S. puniceus*	H. J. Kutzner; DSM 40083. ATCC 19801
	Strains assigned to cluster 10 (*Streptomyces fulvissimus*)	
ISP 5080	*Streptomyces aureoverticillatus*	H. J. Kutzner; DSM 40080. ATCC 15854
ISP 5593	*S. fulvissimus*	A. Seino; KCC S-0754. ATCC 27431
ISP 5599	*S. longispororuber*	A. Seino; KCC S-0784. ATCC 27443
*ISP 5441	'*S. nobilis*'	A. Seino; KCC S-0798. ATCC 19251
*ISP 5512	*S. spectabilis*	A. Seino; KCC S-0832
N735/C, N735/O		T. Schupp, Ciba–Geigy Ltd, Postfach, CH-4002 Basel, Switzerland; UC 2472;† UC 2472†
N739/O, N739/P	*Streptomyces* spp.	T. Schupp; B44/P1; B44/P1
	Strains assigned to cluster 11 (*Streptomyces prunicolor*)	
ISP 5335	*Streptomyces prunicolor*	I. J. Bousfield; NCIB 9978. ATCC 25487
F50	*Streptomyces* sp.	S. T. Williams; F50, soil isolate
	Strains assigned to cluster 12 (*Streptomyces rochei*)	
ISP 5034	'*Streptomyces aerocolonigenes*'	A. Seino; KCC S-0614. ATCC 23870
ISP 5003	*S. albogriseolus*	I. J. Bousfield; NCIB 9812. ATCC 23875
ISP 5465	'*S. alborubidus*'	W. Kuryłowicz; ATCC 23612
ISP 5092	*S. althioticus*	H. J. Kutzner; DSM 40092. ATCC 19724
ISP 5252	*S. arabicus*	A. Seino; KCC S-0682. ATCC 23881
ISP 5010	*S. calvus*	T. Cross; CUB 479. ATCC 13382
ISP 5430	*S. griseoaurantiacus*	A. Seino; KCC S-0763. ATCC 19840
ISP 5191	*S. griseofuscus*	S. T. Williams; A107. ATCC 23916
ISP 5159	*S. griseomycini*	I. J. Bousfield; NCIB 9845. ATCC 23625
ISP 5160	*S. griseorubens*	I. J. Bousfield; NCIB 9846. ATCC 19909
ISP 5124	*S. indigoferus*	W. Kuryłowicz; ATCC 23924
ISP 5433	'*S. lazureus*'	A. Seino; KCC S-0780. ATCC 19843
ISP 5167	'*S. malachiticus*'	H. J. Kutzner; DSM 40167. ATCC 19918
ISP 5188	*S. matensis*	S. T. Williams; A109. ATCC 23935
ISP 5169	*S. mutabilis*	H. J. Kutzner; DSM 40169. ATCC 19919
ISP 5048	*S. parvullus*	H. J. Kutzner; DSM 40048. ATCC 12434
ISP 5319	*S. plicatus*	A. Seino; KCC S-0504. ATCC 25483
ISP 5026	*S. pseudogriseolus*	I. J. Bousfield; NCIB 9814. ATCC 12770
*ISP 5566	'*S. pulcher*'	A. Seino; KCC S-0817. ATCC 13849
ISP 5231	*S. rochei*	A. Seino; KCC S-0668. ATCC 10739
ISP 5177	*S. rubiginosus*	A. Seino; KCC S-0416. ATCC 19927
ISP 5101	*S. tendae*	I. J. Bousfield; NCIB 9814. ATCC 19812
ISP 5179	*S. variabilis*	H. J. Kutzner; DSM 40179. ATCC 19930
ISP 5470	*S. vinaceusdrappus*	A. Seino; KCC S-0529. ATCC 25511
ISP 5486	*S. werraensis*	A. Seino; KCC S-0860. ATCC 14424
202	*Streptomyces* sp.	S. T. Williams; LIV 202
	Strains assigned to cluster 13 (*Streptomyces cellulosae*)	
ISP 5362	*Streptomyces cellulosae*	A. Seino; KCC S-0462. ATCC 25439
ISP 5274	*S. griseoincarnatus*	S. T. Williams; A119. ATCC 23523

Table 1 (*continued*)

	Strains assigned to cluster 14 (*Streptomyces aureofaciens*)	
ISP 5127	*Streptomyces aureofaciens*	S. T. Williams; A28. ATCC 10762
ISP 5172	*S. roseofulvus*	H. J. Kutzner; DSM 40172. ATCC 19921
	Strains assigned to cluster 15 (*Streptomyces chromofuscus*)	
*ISP 5270	*Chainia flava*	A. Seino; KCC S-0751. ATCC 19347
ISP 5301	*C. minutisclerotica*	A. Seino; KCC S-0790. ATCC 17757
ISP 5226	*Streptomyces argenteolus*	I. J. Bousfield; NCIB 9625. ATCC 11009
ISP 5294	'*S. carnosus*'	R. Locci; IPV 1817. ATCC 25437
ISP 5273	*S. chromofuscus*	A. Seino; KCC S-0354. ATCC 23896
ISP 5089	*S. galbus*	W. Kuryłowicz; ATCC 23910
G3	*S. griseus*	L. J. Nisbet; C1943†
ISP 5365	'*S. thermophilus*'	A. Seino; KCC S-0842. ATCC 19282
*ISP 5243	*S. viridosporus*	A. Seino; KCC S-0859. ATCC 27479
	Strains assigned to cluster 16 (*Streptomyces albus*)	
ISP 5313	*Streptomyces albus*	T. Cross; CUB 310. ATCC 3004
ISP 5447	*S. almquistii*	A. Seino; KCC S-0451. ATCC 618
ISP 5186	*S. aminophilus*	I. J. Bousfield; NCIB 9827. ATCC 14961
ISP 5057	*S. cacaoi*	I. J. Bousfield; NCIB 9626. ATCC 3082
ISP 5327	*S. flocculus*	W. Kuryłowicz; ATCC 25453
*ISP 5020	'*S. fungicidicus*'	A. Seino; KCC S-0755. ATCC 27432
	Strains assigned to cluster 17 (*Streptomyces griseoviridis*)	
*ISP 5420	*Streptomyces chryseus*	A. Seino; KCC S-0737. ATCC 19829
ISP 5149	*S. daghestanicus*	H. J. Kutzner; DSM 40149. ATCC 23620
ISP 5229	*S. griseoviridis*	I. J. Bousfield; NCIB 9853. ATCC 23920
ISP 5091	*S. murinus*	H. J. Kutzner; DSM 40091. ATCC 19788
ISP 5533	'*S. rosa*'	A. Seino; KCC S-0822. ATCC 27462
ISP 5240	'*S. roseo-luteus*'	I. J. Bousfield; NCIB 9854. ATCC 23957
	Strains assigned to cluster 18 (*Streptomyces cyaneus*)	
MAV	*Actinsporangium violaceum*	A. Seino; KCC S-0052. ATCC 15813
ISP 5228	*Streptomyces afghaniensis*	W. Kuryłowicz; ATCC 23871
ISP 5293	*S. arenae*	A. Seino; KCC S-0452. ATCC 25428
ISP 5106	*S. azureus*	H. J. Kutzner; DSM 40106. ATCC 14921
ISP 5185	*S. bellus*	S. T. Williams; A106. ATCC 14925
ISP 5140	'*S. bicolor*'	H. J. Kutzner; DSM 40140. ATCC 23614
ISP 5084	*S. caelestis*	I. J. Bousfield; NCIB 9751. ATCC 15084
ISP 5085	*S. chartreusis*	H. J. Kutzner; DSM 40085. ATCC 14922
ISP 5467	*S. cinnabarinus*	S. T. Williams; A159. ATCC 23617
ISP 5144	*S. coeruleofuscus*	H. J. Kutzner; DSM 40144. ATCC 23618
ISP 5145	*S. coeruleorubidus*	S. T. Williams; A104. ATCC 13740
ISP 5146	*S. coerulescens*	I. J. Bousfield; NCIB 9616. ATCC 19896
*ISP 5129	*S. collinus*	H. J. Kutzner; DSM 40129. ATCC 19743
ISP 5107	*S. curacoi*	H. J. Kutzner; DSM 40107. ATCC 13385
*ISP 5108	*S. cyaneus*	S. T. Williams; A13. ATCC 14923
ISP 5013	*S. echinatus*	S. T. Williams; A77. ATCC 19748
ISP 5154	*S. fumanus*	A. Seino; KCC S-0497. ATCC 19904
ISP 5499	*S. griseochromogenes*	A. Seino; KCC S-0746. ATCC 14511
ISP 5469	*S. griseorubiginosus*	A. Seino; KCC S-0481. ATCC 23627
*ISP 5042	*S. hawaiiensis*	I. J. Bousfield; NCIB 9410. ATCC 12236
ISP 5482	*S. iakyrus*	A. Seino; KCC S-0773. ATCC 15375
ISP 5432	'*S. indigocolor*'	A. Seino; KCC S-0774. ATCC 19842
ISP 5206	*S. janthinus*	A. Seino; KCC S-0387. ATCC 15870
ISP 5090	*S. lanatus*	H. J. Kutzner; DSM 40090. ATCC 19775
ISP 5166	*S. longisporus*	R. Locci; IPV 1784. ATCC 23931
ISP 5483	*S. luteogriseus*	A. Seino; KCC S-0796. ATCC 15072
ISP 5588	*S. neyagawaensis*	A. Seino; KCC S-0796. ATCC 27449
ISP 5531	'*S. pallidus*'	A. Seino; KCC S-0810. ATCC 27457
ISP 5592	'*S. peruviensis*'	A. Seino; KCC S-0813. ATCC 27459
ISP 5212	*S. pseudovenezuelae*	W. Kuryłowicz; ATCC 23951
ISP 5310	*S. purpurascens*	A. Seino; KCC S-0509. ATCC 25489
ISP 5133	*S. resistomycificus*	I. J. Bousfield; NCIB 9843. ATCC 19804

Table 1 (*continued*)

ISP 5277	*S. roseviolaceus*	A. Seino; KCC S-0513. ATCC 25493
ISP 5227	'*S. thermotolerans*'	A. Seino; KCC S-0519. ATCC 11416
ISP 5205	*S. violarus*	A. Seino; KCC S-0534. ATCC 25516
ISP 5209	*S. violatus*	A. Seino; KCC S-0851. ATCC 15892
ISP 5207	'*S. violochromogenes*'	W. Kuryłowicz; ATCC 15893
M1	*Streptomyces* sp.	S. T. Williams; M1, soil isolate
	Strains assigned to cluster 19 (*Streptomyces diastaticus*)	
M301	*Microellobosporia cinerea*	T. Cross; CUB 301. ATCC 15840
M315	*M. flavea*	T. Cross; CUB 315. ATCC 15332
ISP 5028	*Streptomyces achromogenes*	R. Locci; IPV 1607. ATCC 12767
ISP 5262	*S. bottropensis*	A. Seino; KCC S-0459. ATCC 25435
ISP 5256	'*S. coralus*'	I. J. Bousfield; NCIB 9802. ATCC 23901
*ISP 5496	*S. diastaticus*	A. Seino; KCC S-0745. ATCC 3315
ISP 5449	*S. diastatochromogenes*	A. Seino; KCC S-0746. ATCC 12309
ISP 5481	*S. galilaeus*	A. Seino; KCC S-0757. ATCC 14969
ISP 5429	*S. glomeraurantiacus*	A. Seino; KCC S-0761. ATCC 19839
ISP 5263	*S. humidus*	A. Seino; KCC S-0386. ATCC 12760
ISP 5355	*S. lincolnesis*	R. Locci; IPB 1848. ATCC 25466
ISP 5031	'*S. minoensis*'	H. J. Kutzner; DSM 40031. ATCC 19787
ISP 5553	*S. mirabilis*	A. Seino; KCC S-0791. ATCC 27447
ISP 5490	'*S. nigellus*'	A. Seino; KCC S-0797. ATCC 27450
ISP 5451	*S. olivochromogenes*	A. Seino; KCC S-0500. ATCC 3336
*ISP 5285	*S. phaeoviridis*	I. J. Bousfield; NCIB 9832. ATCC 23947
ISP 5489	*S. rishiriensis*	A. Seino; KCC S-0821. ATCC 14812
ISP 5560	'*S. tauricus*'	A. Seino; KCC S-0837. ATCC 27470
ISP 5309	*S. vastus*	A. Seino; KCC S-0524. ATCC 25506
F1	*Streptomyces* sp.	S. T. Williams; F1, soil isolate
	Strains assigned to cluster 20 (*Streptomyces olivaceoviridis*)	
M086	*Elytrosporangium brasiliense*	A. Seino; KCC S-0086. ATCC 23727
M619	*E. carpinense*	T. Cross; CUB 619
M09A	*E. spirale*	T. Cross; CUB 639. ATCC 25664
ISP 5528	*Streptomyces canarius*	A. Seino; KCC S-0733. ATCC 27423
ISP 5340	*S. corchorusii*	I. J. Bousfield; NCIB 9979. ATCC 25444
*ISP 5334	*S. olivaceoviridis*	A. Seino; KCC S-0499. ATCC 23630
ISP 5551	*S. regensis*	A. Seino; KCC S-0820. ATCC 27461
	Strains assigned to cluster 21 (*Streptomyces griseoruber*)	
E35	*Actinopycnidium caeruleum*	U.S.S.R. Research Institute for Antibiotics, Napatinskaya ul. 3a, Moscow B-105, U.S.S.R.; RIA 729
*ISP 5419	'*Streptomyces caesius*'	A. Seino; KCC S-0731. ATCC 19828
*ISP 5421	*S. coelescens*	A. Seino; KCC S-0739. ATCC 19830
ISP 5425	'*S. cyanocolor*'	W. Kuryłowicz; ATCC 19833
ISP 5275	*S. griseoruber*	W. Kuryłowicz; ATCC 23626†
ISP 5281	*S. griseoruber*	A. Seino; KCC S-0642. ATCC 23919
ISP 5434	'*S. lividans*'	A. Seino; KCC S-0783. ATCC 19844
ISP 5505	*S. tuirus*	A. Seino; KCC S-0846. ATCC 19007
ISP 5438	*S. violaceolatus*	A. Seino; KCC S-0531. ATCC 19847
	Strains assigned to cluster 22 ('*Chainia*' *poonensis*)	
ISP 5596	'*Chainia*' *poonensis*	A. Seino; KCC S-0815. ATCC 15723
ISP 5303	*C. rosea*	T. Cross; CUB 596. ATCC 17755
	Strains assigned to cluster 23 (*Streptomyces microflavus*)	
ISP 5053	*Streptomyces ambofaciens*	A. Seino; KCC S-0618. ATCC 23877
ISP 5014	*S. eurythermus*	R. Locci; IPV 1606. ATCC 14975
ISP 5562	*S. griseosporeus*	A. Seino; KCC S-0766. ATCC 27435
*ISP 5313	*S. microflavus*	T. Cross; CUB 310. ATCC 13231
ISP 5115	*S. recifensis*	H. J. Kutzner; DSM 40. ATCC 19803

Table 1 (*continued*)

	Strains assigned to cluster 24 (*Streptomyces flaveolus*)	
ISP 5220	*Streptomyces chibaensis*	A. Seino; KCC S-0632. ATCC 23895
ISP 5061	*S. flaveolus*	H. J. Kutzner; DSM 40061. ATCC 3319
ISP 5244	*S. xantholiticus*	A. Seino; KCC S-0863. ATCC 27481
	Strains assigned to cluster 25 (*Streptomyces canus*)	
ISP 5017	*Streptomyces canus*	I. J. Bousfield; NCIB 9807. ATCC 12237
ISP 5511	'*S. ostreogriseus*'	S. T. Williams; A166. ATCC 27455
	Strains assigned to cluster 26 (*Streptomyces graminofaciens*)	
ISP 5559	*Streptomyces graminofaciens*	A. Seino; KCC S-0762. ATCC 12705
ISP 5338	'*S. pristinaespiralis*'	A. Seino; KCC S-0507. ATCC 25486
	Strains assigned to cluster 27 (*Streptomyces viridochromogenes*)	
*ISP 5110	*Streptomyces viridochromogenes*	A. Seino; KCC S-0856. ATCC 14920
*ISP 5381	'*S. viridis*'	A. Seino; KCC S-0854. ATCC 15732
	Strains assigned to cluster 28 (*Streptomyces glaucescens*)	
ISP 5153	'*Streptomyces flavoviridis*'	H. J. Kutzner; DSM 40153. ATCC 19903
ISP 5155	*S. glaucescens*	A. Seino; KCC S-0377. ATCC 23622
	Strains assigned to cluster 29 (*Streptomyces lydicus*)	
ISP 5492	*Streptomyces albulus*	A. Seino; KCC S-0718. ATCC 12757
ISP 5054	'*S. fasiculatus*'	H. J. Kutzner; DSM 40054. ATCC 19751
ISP 5009	*S. griseoplanus*	I. J. Bousfield; NCIB 9811. ATCC 19766
*ISP 5555	*S. libani*	A. Seino; KCC S-0781. ATCC 23732
ISP 5461	*S. lydicus*	W. Kuryłowicz; ATCC 25470
*ISP 5357	'*S. natalensis*'	A. Seino; KCC S-0693. ATCC 27448
ISP 5276	*S. nigrescens*	I. J. Bousfield; NCIB 9856. ATCC 23941
ISP 5041	*S. platensis*	A. Seino; KCC S-0662. ATCC 23948
ISP 5241	'*S. saraceticus*'	A. Seino; KCC S-0877. ATCC 25496
ISP 5032	*S. sioyaensis*	H. J. Kutzner; DSM 40032. ATCC 13989
ISP 5030	'*S. toyocaensis*'	I. J. Bousfield; NCIB 9808. ATCC 19814
	Strains assigned to cluster 30 (*Streptomyces filipinensis*)	
ISP 5539	*Streptomyces durhamensis*	A. Seino; KCC S-0747. ATCC 23194
ISP 5112	*S. filipinensis*	A. Seino; KCC S-0369. ATCC 23905
*ISP 5572	'*S. gannmycicus*'	A. Seino; KCC S-0759. ATCC 27434
*ISP 5224	'*S. yokosukanensis*'	A. Seino; KCC S-0559. ATCC 25520
	Strains assigned to cluster 31 (*Streptomyces antibioticus*)	
ISP 5234	*Streptomyces antibioticus*	A. Seino; KCC S-0620. ATCC 8663
ISP 5317	*S. lucensis*	A. Seino; KCC S-0490. ATCC 17804
ISP 5306	*S. misionensis*	A. Seino; KCC S-0497. ATCC 14991
ISP 5282	*S. naganishii*	A. Seino; KCC S-0654. ATCC 23939
ISP 5367	*S. phaeofaciens*	A. Seino; KCC S-0814. ATCC 15034
	Strains assigned to cluster 32 (*Streptomyces violaceoniger*)	
ISP 5187	*Streptomyces endus*	I. J. Bousfield; NCIB 9819. ATCC 23904
ISP 5578	*S. hygroscopicus*	A. Seino; KCC S-0772. ATCC 27438
N736	*S. hygroscopicus*	T. Schupp; UC 5208†
ISP 5318	*S. melanosporofaciens*	A. Seino; KCC S-0485. ATCC 25473
ISP 5356	*S. sparsogenes*	A. Seino; KCC S-0517. ATCC 25498
*ISP 5563	*S. violaceoniger*	A. Seino; KCC S-0850. ATCC 27477
	Strains assigned to cluster 33 ('*Streptomyces chromogenus*')	
*ISP 5475	'*Streptomyces atrofaciens*'	A. Seino; KCC S-0724. ATCC 27418
ISP 5384	'*S. chromogenus*'	A. Seino; KCC S-0736. ATCC 27424
ISP 5192	*S. melanogenes*	I. J. Bousfield; NCIB 9835. ATCC 23937
ISP 5223	*S. noboritoensis*	A. Seino; KCC S-0065. ATCC 25477
ISP 5242	'*S. umbrosus*'	A. Seino; KCC S-0522. ATCC 25504

Table 1 (*continued*)

	Strains assigned to cluster 34 (*Streptomyces nogalater*)	
ISP 5487	'*Streptomyces lavenduligriseus*'	A. Seino; KCC S-0779. ATCC 13306
ISP 5546	*S. nogalater*	A. Seino; KCC S-0553. ATCC 27451
*ISP 5476	'*S. spadicis*'	A. Seino; KCC S-0831. ATCC 19017
	Strains assigned to cluster 35 (*Streptomyces chattanoogensis*)	
ISP 5002	*Streptomyces chattanoogensis*	I. J. Bousfield; NCIB 9809. ATCC 13358
ISP 5109	*S. nodosus*	A. Seino; KCC S-0656. ATCC 14899
	Strains assigned to cluster 36 (*Streptomyces thermovulgaris*)	
ISP 5574	'*Streptomyces thermoflavus*'	A. Seino; KCC S-0315. ATCC 27473
ISP 5579	*S. thermonitrificans*	A. Seino; KCC S-0841. ATCC 23385
ISP 5444	*S. thermovulgaris*	A. Seino; KCC S-0520. ATCC 19284
	Strains assigned to cluster 37 (*Streptomyces griseoflavus*)	
ISP 5198	*Streptomyces cyanoalbus*	S. T. Williams; A108. ATCC 15859
ISP 5456	*S. griseoflavus*	W. Kuryłowicz; ATCC 25456
ISP 5095	*S. hirsutus*	H. J. Kutzner; DSM 40095. ATCC 19773
ISP 5097	*S. pilosus*	H. J. Kutzner; DSM 40097. ATCC 19797
ISP 5098	*S. prasinopilosus*	I. J. Bousfield; NCIB 9842. ATCC 19799
ISP 5099	*S. prasinus*	H. J. Kutzner; DSM 40099. ATCC 19800
	Strains assigned to cluster 38 (*Streptomyces prasinosporus*)	
*ISP 5096	'*Streptomyces macrosporeus*'	A. Seino; KCC S-0145. ATCC 19783
ISP 5506	*S. prasinosporus*	A. Seino; KCC S-0816. ATCC 17918
ISP 5547	'*S. steffisburgensis*'	A. Seino; KCC S-0833. ATCC 27466
	Strains assigned to cluster 39 (*Streptomyces longisporoflavus*)	
ISP 5564	*Streptomyces bluensis*	A. Seino; KCC S-0729. ATCC 27420
ISP 5165	*S. longisporoflavus*	H. J. Kutzner; DSM 40165. ATCC 19915
ISP 5605	'*S. tumuli*'	A. Seino; KCC S-0847. ATCC 27474
	Strains assigned to cluster 40 (*Streptomyces phaeochromogenes*)	
ISP 5269	*Chainia antibiotica*	A. Seino; KCC S-0828. ATCC 15721
ISP 5302	*C. nigra*	T. Cross; CUB 595. ATCC 17756
ISP 5271	*C. purpurogena*	A. Seino; KCC S-0818. ATCC 19348
ISP 5597	*C. violens*	A. Seino; KCC S-0852. ATCC 15898
ISP 5073	*Streptomyces phaeochromogenes*	S. T. Williams; A25. ATCC 3338
ISP 5079	'*S. verne*'	A. Seino; KCC S-0527. ATCC 3353
	Strains assigned to cluster 41 (*Chainia ochracea*)	
ISP 5594	*Chainia ochracea*	A. Seino; KCC S-0801. ATCC 15814
N745	*Saccharopolyspora hirsuta*	J. Lacey, Dept for Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts., U.K.; A1143
	Single member clusters	
N950	*Nocardioides albus*	H. Prauser; IMET 7801. ATCC 27980
ISP 5197	'*Streptomyces albocyaneus*'	W. Kuryłowicz; ATCC 15845
ISP 5138	*S. aurantiogriseus*	I. J. Bousfield; NCIB 9849. ATCC 19887
ISP 5590	*S. bambergiensis*	A. Seino; KCC S-0728. ATCC 13879
ISP 5065	*S. gelaticus*	I. J. Bousfield; NCIB 9848. ATCC 3323
ISP 5529	'*S. moderatus*'	A. Seino; KCC S-0792. ATCC 23443
ISP 5491	'*S. versipellis*'	A. Seino; KCC S-0848. ATCC 27475
	Cluster-group B	
	Strains assigned to cluster 42 (*Streptomyces rimosus*)	
ISP 5268	*Streptomyces albofaciens*	W. Kuryłowicz; ATCC 25184
*ISP 5535	*S. anandii*	A. Seino; KCC S-0720. ATCC 19388
ISP 5402	'*S. capuensis*'	W. Kuryłowicz; ATCC 25436
ISP 5545	*S. chrestomyceticus*	A. Seino; KCC S-0735. ATCC 14947
ISP 5366	'*S. flavofungini*'	A. Seino; KCC S-0753. ATCC 27430
ISP 5500	*S. kanamyceticus*	A. Seino; KCC S-0775. ATCC 12853
ISP 5260	*S. rimosus*	T. Cross, CUB 205. ATCC 10970

Table 1 (*continued*)

	Single member cluster	
ISP 5219	*Streptomyces amakusaensis*	A. Seino; KCC S-0671. ATCC 23876
	Cluster-group C	
	Strains assigned to cluster 24 (*Streptomyces griseoluteus*)	
ISP 5258	*Streptomyces catenulae*	W. Kuryłowicz; ATCC 12476
ISP 5480	*S. galbus*	A. Seino; KCC S-0327. ATCC 14077
ISP 5392	*S. griseoluteus*	A. Seino; KCC S-0765. ATCC 12768
	Strains assigned to cluster 44 (*Streptomyces pactum*)	
*ISP 5345	'*Streptomyces karnatakensis*'	A. Seino; KCC S-0485. ATCC 25463
*ISP 5568	*S. lusitanus*	A. Seino; KCC S-0785. ATCC 27444
ISP 5530	*S. pactum*	A. Seino; KCC S-0809. ATCC 27456
	Strains assigned to cluster 45 (*Streptomyces aurantiacus*)	
ISP 5412	*Streptomyces aurantiacus*	A. Seino; KCC S-0453. ATCC 19822
ISP 5494	*S. capoamus*	A. Seino; KCC S-0734. ATCC 19006
ISP 5443	*S. thermoviolaceus*	A. Seino; KCC S-0780. ATCC 19283
	Strains assigned to cluster 46 (*Streptomyces varsoviensis*)	
ISP 5567	'*Streptomyces paraguayensis*'	T. Cross; CUB 498. ATCC 27458
ISP 5346	*S. varsoviensis*	T. Cross; CUB 308. ATCC 14681
	Strains assigned to cluster 47 (*Streptomyces tubercidicus*)	
G1	'*Streptomyces cattleya*'	L. J. Nisbet; C2201
ISP 5261	*S. tubercidicus*	W. Kuryłowicz; ATCC 25502
	Single member clusters	
ISP 5139	*Streptomyces badius*	R. Locci; IPV 1613. ATCC 19888
ISP 5100	*S. ramulosus*	H. J. Kutzner; DSM 40100. ATCC 19802
*ISP 5104	*S. sulphureus*	A. Seino; KCC S-0835. ATCC 27468
	Cluster-group D	
	Single member clusters	
M297	*Microellobosporia violacea*	T. Cross; CUB 297. ATCC 15332
ISP 5035	*Streptomyces massasporeus*	H. J. Kutzner; DSM 40035. ATCC 19785
	Cluster-group E	
	Strains assigned to cluster 48 ('*Streptomyces pyridomyceticus*')	
ISP 5024	'*Streptomyces pyridomyceticus*'	A. Seino; KCC S-0666. ATCC 23953
A87	'Cluster A'	J. Lacey; A1016
	Strains assigned to cluster 49 ('Cluster A/B')	
A84	'Cluster A'	J. Lacey; A470
A53	'Cluster B'	J. Lacey; A670
	Strains assigned to cluster 50 (*Actinomadura* spp.)	
A16	*Actinomadura madurae*	NCTC 5654
A17	*A. madurae*	NCTC 1070†
A3	*A. pusilla*	H. Nonomura, Faculty of Engineering, Yamanashi University, Kofu, Japan; A-118. ATCC 27296
A2	*A. roseoviolacea*	H. Nonomura; A-5. ATCC 27297
A4	*A. verrucosospora*	H. Nonomura; A-184. ATCC 27299
E63	*Microtetraspora glauca*	ATCC 23057
	Strains assigned to cluster 51 (Acidophilic isolates)	
MR10, MR19	Acidophilic soil isolates	S. T. Williams; MR10, MR19
	Strains assigned to cluster 52 (*Nocardia* spp.)	
N317	*Nocardia asteroides*	ATCC 19247
ISP 5040	'*N.*' *orientalis*	A. Seino; KCC S-0662. ATCC 19795

Table 1 (*continued*)

	Strains assigned to cluster 53 ('*Nocardia*' *mediterranea*)	
N730	'*Nocardia*' *mediterranea*	T. Schupp; ATCC 13685
N731, N732, N733	'*N.*' *mediterranea*	T. Schupp; T5; T87; MER/973
ISP 5501	'*Streptomyces mediterranei*'	A. Seino; KCC S-0789
N737, N738	'*S. tolypophorus*'	T. Schupp; IFO/2554; ATCC 2117†
N734	*Streptomyces* sp.	T. Schupp; U.S. patent strain 3871966
	Strains assigned to cluster 54 (*Streptomyces alboflavus*)	
ISP 5045	*Streptomyces alboflavus*	A. Seino; KCC S-0615. ATCC 12626
ISP 5414	'*S. aureofasciculus*'	W. Kuryłowicz; ATCC 19824
ISP 5435	'*S. longissimus*'	A. Seino; KCC S-0489. ATCC 19850
	Single member cluster	
A5	*Actinomadura helvata*	H. Nonomura; A-105. ATCC 27295
	Cluster-group F	
	Strains assigned to cluster 55 (*Streptoverticillium griseocarneum*)	
ISP 5315	'*Streptomyces paucisporogenes*'	A. Seino; KCC S-0857. ATCC 12596
ISP 5520	'*S. tropicalensis*'	A. Seino; KCC S-0845. ATCC 17963
ISP 5005	*Streptoverticillium cinnamoneum*	R. Locci; IPV 1776. ATCC 11874
ISP 5004	*Stv. griseocarneum*	H. J. Kutzner; DSM 40004. ATCC 12628
ISP 5114	*Stv. hachijoense*	R. Locci; IPV 2057. ATCC 19769
ISP 5038	*Stv. luteoverticillatum*	H. J. Kutzner; DSM 40038. ATCC 23933
M640	*Stv. luteoverticillatum*	T. Cross; CUB 604. ATCC 23933
ISP 5221	*Stv. mashuense*	H. J. Kutzner; DSM 40221. ATCC 23934
ISP 5577	*Stv. septatum*	A. Seino; KCC S-0829. ATCC 27464
	Strains assigned to cluster 56 (*Streptoverticillium netropsis*)	
ISP 5526	*Streptomyces avidinii*	A. Seino; KCC S-0726. ATCC 27419
ISP 5604	*Streptoverticillium eurocidicum*	A. Seino; KCC S-0749. ATCC 27428
ISP 5093	*Stv. flavopersicum*	H. J. Kutzner; DSM 40093. ATCC 19756
ISP 5259	*Stv. netropsis*	S. T. Williams; A79. ATCC 23940
	Strains assigned to cluster 57 (*Streptoverticillium hiroshimense*)	
ISP 5037	*Streptoverticillium hiroshimense*	I. J. Bousfield; NCIB 9839. ATCC 1977
ISP 5436	*Stv. rectiverticillatum*	R. Locci; IRV 1852. ATCC 19845
	Strains assigned to cluster 58 (*Streptoverticillium blastmyceticum*)	
ISP 5604	'*Streptomyces caespitosus*'	A. Seino; KCC S-0732. ATCC 27422
ISP 5029	*Streptoverticillium blastmyceticum*	I. J. Bousfield; NCIB 9800. ATCC 1973
ISP 5507	*Stv. griseoverticillatum*	R. Locci; IPV 1976. ATCC 27436
M638	*Stv. mobaraense*	T. Cross; CUB 638. ATCC 29032
ISP 5571	*Stv. orinoci*	T. Cross; CUB 602. ATCC 23202
	Strains assigned to cluster 59 (*Streptoverticillium biverticillatum*)	
ISP 5565	'*Streptomyces aspergilloides*'	A. Seino; KCC S-0723. ATCC 14808
ISP 5503	'*S. moro-okaensis*'	A. Seino; KCC S-0793. ATCC 19166
M635	*Streptoverticillium biverticillatum*	T. Cross; CUB 635. ATCC 23615
	Strains assigned to cluster 60 ('*Streptoverticillium griseostramineus*')	
ISP 5161	'*Streptoverticillium griseostramineus*'	H. J. Kutzner; DSM 40161. ATCC 23628
ISP 5162	'*Stv. kurssanovii*'	H. J. Kutzner; DSM 40162. ATCC 15824

Table 1 (*continued*)

	Strains assigned to cluster 61 (*Streptomyces lavendulae*)	
*ISP 5558	*Streptomyces colombiensis*	A. Seino; KCC S-0740. ATCC 27425
ISP 5152	*S. flavotricini*	H. J. Kutzner; DSM 40152. ATCC 23621
*ISP 5190	*S. goshikiensis*	S. T. Williams; A105. ATCC 23914
*ISP 5550	*S. katrae*	A. Seino; KCC S-0777. ATCC 27440
ISP 5069	*S. lavendulae*	S. T. Williams; A38. ATCC 8664
ISP 5216	*S. lavendulocolor*	S. T. Williams; A121. ATCC 15871
ISP 5316	*S. polychromogenes*	A. Seino; KCC S-0236. ATCC 12595
ISP 5194	*S. racemochromogenes*	A. Seino; KCC S-0407. ATCC 23954
*ISP 5445	*S. subrutilus*	A. Seino; KCC S-0834. ATCC 27467
ISP 5178	*S. toxytricini*	I. J. Bousfield; NCIB 9847. ATCC 19813
ISP 5094	*S. virginiae*	H. J. Kutzner; DSM 40094. ATCC 19817
ISP 5134	*S. xanthophaeus*	H. J. Kutzner; DSM 40134. ATCC 19819
	Strains assigned to cluster 62 (*Streptomyces luridus*)	
ISP 5479	*Streptomyces cirratus*	A. Seino; KCC S-0738. ATCC 14699
ISP 5431	*S. helvaticus*	A. Seino; KCC S-0768. ATCC 19841
ISP 5081	*S. luridus*	H. J. Kutzner; DSM 40081. ATCC 19782
	Strains assigned to cluster 63 (*Streptomyces xanthochromogenes*)	
*ISP 5570	*Streptomyces albolongus*	A. Seino; KCC S-0716. ATCC 27414
ISP 5111	*S. xanthochromogenes*	A. Seino; KCC S-0612. ATCC 19818
F6	*Streptomyces* sp.	S. T. Williams; F6; soil isolate
	Strains assigned to cluster 64 (*Streptomyces bikiniensis*)	
ISP 5581	*Streptomyces bikiniensis*	A. Seino; KCC S-0011. ATCC 11062
SW1	*Streptomyces* sp.	S. T. Williams; SW1; acidophilic soil isolate
	Strains assigned to cluster 65 (*Kitasatoa* spp.)	
Ka 280	*Kitasatoa diplospora*	A. Matsumae; KI 104075. ATCC 27788
Ka 281	*K. kauaiensis*	A. Matsumae; KI 104076. ATCC 21405
Ka 282	*K. nagasakiensis*	A. Matsumae; KI 104077. ATCC 27789
Ka 279	*K. purpurea*	S. Matsumae; KI 104078. ATCC 27787
	Strains assigned to cluster 66 (*Streptomyces misakiensis*)	
ISP 5222	*Streptomyces misakiensis*	I. J. Bousfield; NCIB 9852. ATCC 23938
*ISP 5239	'*S. viridifaciens*'	A. Seino; KCC S-0853. ATCC 11989
*ISP 5575	*S. xanthocicidicus*	A. Seino; KCC S-0862. ATCC 27480
	Strains assigned to cluster 67 (*Streptomyces psammoticus*)	
*ISP 5554	*Streptomyces avellaneus*	A. Seino; KCC S-0725. ATCC 23730
ISP 5341	*S. psammoticus*	A. Seino; KCC S-0434. ATCC 25488
	Single member clusters	
ISP 5021	'*Streptomyces mediocidicus*'	I. J. Bousfield; NCIB 9836. ATCC 23936
ISP 5051	*Streptoverticillium albirecticuli*	A. Seino; KCC S-0116. ATCC 19721
M636	*Stv. baldaccii*	T. Cross; CUB 636. ATCC 23654
ISP 5052	*Stv. kentuckense*	R. Locci; IPV 1780. ATCC 12691
ISP 5587	*Stv. ladakanum*	A. Seino; KCC S-0778. ATCC 27441
ISP 5027	*Stv. thioluteum*	A. Seino; KCC S-0844. ATCC 12310
	Cluster-group G	
	Strains assigned to cluster 68 (*Streptomyces fradiae*)	
ISP 5063	*Streptomyces fradiae*	A. Seino; KCC S-0579. ATCC 10745
ISP 5173	*S. roseolilacinus*	A. Seino; KCC S-0335. ATCC 19922
	Single member cluster	
ISP 5044	*Streptomyces fragilis*	I. J. Bousfield; NCIB 9795. ATCC 23908
	Cluster-group H	
	Single member clusters	
ISP 5534	'*Streptomyces cyaneogriseus*'	A. Seino; KCC S-0744. ATCC 27426
ISP 5163	*S. lateritius*	H. J. Kutzner; DSM 40163. ATCC 19913

Table 1 (*continued*)

	Cluster-group I	
	Strains assigned to cluster 69 ('*Nocardia*' *autotrophica*)	
ISP 5011	'*Nocardia*' *autotrophica*	I. J. Bousfield; NCIB 9810. ATCC 19727
*ISP 5472	'*Nocardia salmonicida*'	A. Seino; KCC S-0826. ATCC 27463
	Single member cluster	
ISP 5218	*Streptomyces finlayi*	S. T. Williams; A111. ATCC 23340
	Cluster-group J	
	Strains assigned to cluster 70 ('*Streptomyces viridoflavus*')	
A28	*Streptomyces somaliensis*	F. Mariat, Institut Pasteur, Paris, France; 313
A46	'Cluster B'	J. Lacey; A336
ISP 5237	'*S. viridoflavus*'	A. Seino; KCC S-0857. ATCC 12631
	Strains assigned to cluster 71 (*Streptomyces clavuligerus*)	
G2	*Streptomyces clavuligerus*	L. J. Nisbet; C1838
G4	'*S. jumonijinensis*'	L. J. Nisbet; C2257
	Strains assigned to cluster 72 (Acidophilic isolates)	
H1, MR2, MR22, SW5, SW10	Acidophilic soil isolates	S. T. Williams; H1, MR2, MR22, SW5, SW10
	Strains assigned to cluster 73 (*Actinomadura pelletieri*)	
A19, A20	*Actinomadura pelletieri*	NCTC 4162; NCTC 9999†
	Single member clusters	
IC	*Intrasporangium calvum*	T. Cross; CUB 403. ATCC 23552
ISP 5398	'*Streptomyces luteofluorescens*'	W. Kuryłowicz; ATCC 25469
ISP 5358	*S. novaecaesareae*	A. Seino; KCC S-0800. ATCC 27452
	Single Member Cluster-group	
ISP 5225	'*Nocardia capreola*'	I. J. Bousfield; NCIB 9801. ATCC 27452

Sources: ATCC, American Type Culture Collection, Rockville, Md., U.S.A.; CUB, School of Biological Sciences, University of Bradford, Bradford, U.K.; DSM, Deutsche Sammlung von Mikroorganismen, Teilsammlung Darmstadt, Actinomycetales, Schnittsphanstrasse 9, 61 Darmstadt, F.R.G.; Glaxo, Glaxo-Allenburys Research, Sefton Park, Stoke Poges, Surrey, U.K.; IMET, Akademie der Wissenschaften der D.D.R., Zentralinstitut für Mikrobiologie und Experimentelle Therapie, Beuthenbergstrasse 11, 69 Jena, G.D.R.; IMRU, Institute of Microbiology, Rutgers University, New Brunswick, N.J., U.S.A.; IPV, Istituto di Patologia Vegetale, Cattedra di Micologia, Università degli Studi, Via Celoria, Milan, Italy; KCC, KCC Culture Collection of Actinomycetes, Kaken Chemical Co. Ltd, 6-42, Jujodai 1-Chome, Kita-ku, Tokyo, 114 Japan; KI, Department of Antibiotics, Kitasato Institute, Shirokane 5-Chome, Minato-ku, Tokyo 108, Japan; LIV, Department of Botany, University of Liverpool, Liverpool, U.K.; NCIB, National Collection of Industrial Bacteria, Torry Research Station, P.O. Box 31, 135 Abbey Road, Aberdeen, U.K.; NCTC, National Collection of Type Cultures, Central Public Health Laboratory, Colindale Avenue, London, U.K.

* Duplicate cultures.

† Strain studied was not the type strain.

were defined at the 70·1% similarity (*S*) level and clusters at the 77·5% *S*-levels. These levels were selected, after examination of the dendrograms, as they were the highest which gave clear groupings.

All of the test strains were recovered in ten cluster-groups, A to J (Fig. 1), which were in turn further subdivided into 73 composite and 28 single member clusters (Table 1). The ten cluster-groups encompassed six major taxa, containing six or more strains, and four minor ones accommodating fewer strains. '*Nocardia capreola*' ISP 5225 was not included in any of the cluster-groups.

Of the 303 strains received as *Streptomyces*, 218 fell into cluster-group A; the remainder were distributed amongst the other cluster-groups. Cluster-group A also included representatives of the genera *Actinopycnidium*, *Actinosporangium*, *Chainia*, *Elytrosporangium*, *Microellobosporia* and *Nocardiopsis*, while *Nocardioides albus* N950 and *Saccharopolyspora hirsuta* N745 were located

Table 2. *Reproducibility of groups of tests calculated from comparison of data on the 44 duplicate cultures*

Character states	Test	Agreement between duplicates (%)	Test variance (s^2)
	Morphology and pigmentation:		
1	Presence or absence of spores*	100	0
2–5	Spore chain morphology†	89·2	0·054
6–10	Spore chain ornamentation†	98·2	0·009
11	Presence or absence of aerial spore mass*	95·5	0·023
12–18	Colour of aerial spore mass†	96·4	0·018
19–23	Pigmentation of substrate mycelium†	97·3	0·014
24	Presence or absence of diffusible pigments*	88·6	0·057
25–29	Pigmentation of diffusible pigments†	97·3	0·014
30–31	pH sensitivity of substrate and diffusible pigments	100	0
32	Melanin production on peptone/yeast/iron agar	100	0
33	Melanin production on tyrosine agar	95·5	0·023
34	Fragmentation of mycelium	100	0
35	Sclerotia formation	100	0
66	Sporulation on substrate mycelium	100	0
	Antimicrobial activity:		
54–61	Mean of 5 bacteria, 2 yeasts and 1 fungus	92·6	0·037
	Enzymic activity:		
47–53, 62	Mean of 8 tests	98·8	0·051
63	β-Lactamase production on yeast peptone plus glycerol agar	86·4	0·068
64	β-Lactamase production on Beecham's FS agar	81·8	0·09
65	Production of *Klebsiella* β-lactamase inhibitor	97·7	0·011
	Degradation tests:		
67–84	Mean of 18 substrates	95·3	0·023
	Resistance to antibiotics:		
85–95	Mean of 11 antibiotics	95·5	0·023
96–114	*Growth at various temperatures and in the presence of chemical inhibitors*	93·5	0·032
	Growth on sole nitrogen sources:		
36–46	Mean of 11 sources	86·6	0·067
	Growth on sole carbon sources:		
115–139	Mean of 25 sources	92·2	0·039

* Character essential for determination of relevant multistate character.
† Multistate character.

on the periphery of the group. The second largest cluster-group, F, contained all of the strains received as *Streptoverticillium*, except *Stv. olivoverticillatum* ISP 5250, and a number of *Kitasatoa* and *Streptomyces* species. Cluster-group J included *Actinomadura pelletieri* and a number of streptomycetes, including acidophilic isolates; the remaining actinomaduras fell into cluster-group E together with *Microtetraspora glauca* E63 and some *Nocardia* strains.

Clusters defined at the 77·5% *S*-level were assigned to 22 major (six or more strains) and 51 minor (fewer than six strains) clusters. Phena were named, where possible, after the earliest described species which they contained. Where more than one type strain was described in the same year, the name was selected alphabetically. The same practice was followed for clusters composed of species not cited in the *Approved Lists of Bacterial Names* (Skerman *et al.*, 1980), but in such cases the binomial is given in inverted commas. The relationships between the major clusters and selected minor and single member clusters can be seen in Figs 2 and 3.

Cluster-group A contained 17 major, 24 minor and 7 single member clusters. Cluster-group B had one major cluster, *Streptomyces rimosus*, and *Streptomyces amukusaensis* ISP 5219, while cluster-group C had four minor and three single-member clusters (Table 1). Cluster-group E accommodated two major clusters, which contained *Actinomadura* and *Nocardia* strains, respectively, five minor clusters and *Actinomadura helvata* A5. Cluster-group F contained two major, eleven minor and six single member clusters. The remaining seven minor clusters were

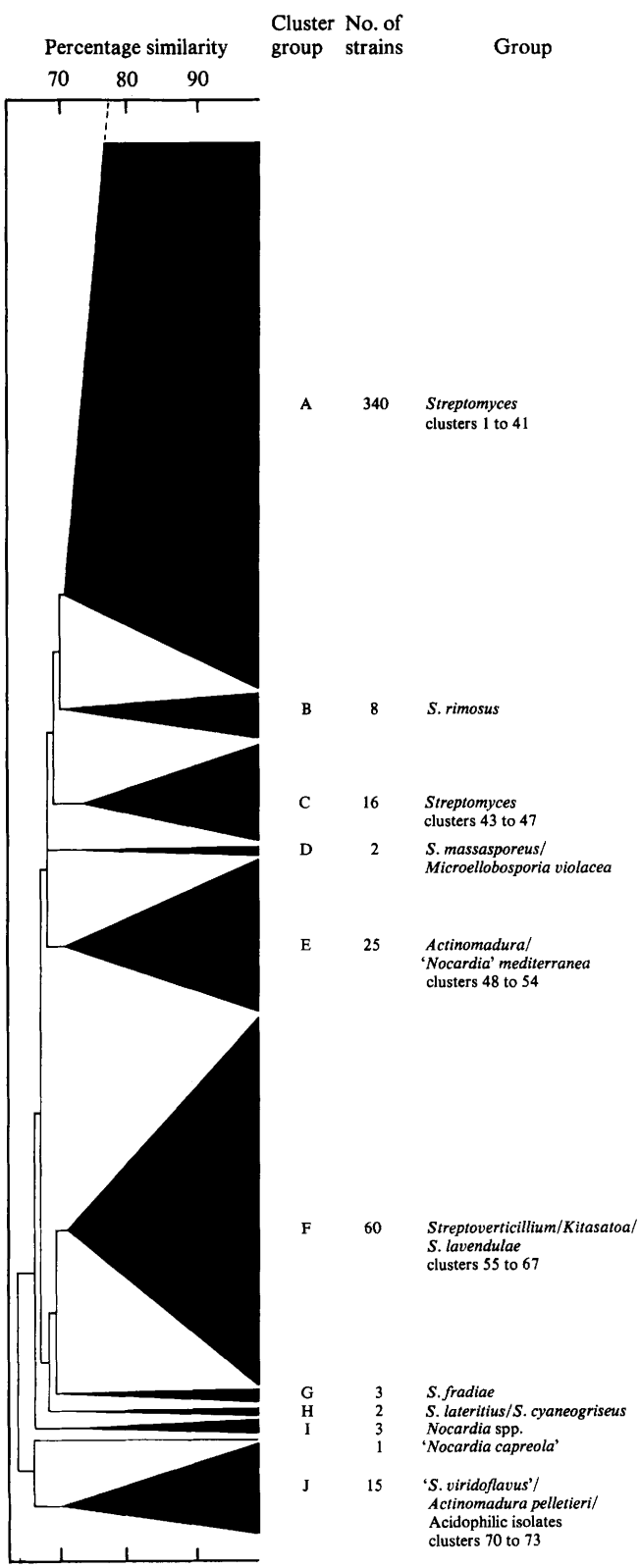


Fig. 1. An abridged dendrogram showing the relationships between cluster-groups defined at the 70·1% similarity level in the S_{SM}/UPGMA analysis.

assigned to cluster-groups G, I and J. The properties of the major and minor cluster-groups and those of '*Nocardia capreola*' ISP 5225 are shown in Table 3.

Most of the major cluster-groups were heterogeneous and therefore it was difficult to select taxon-specific characters (Table 3). Nevertheless, they provided a convenient means of grouping the large number of clusters defined at the higher similarity level.

Composition and characteristics of major clusters. Twenty-two major clusters, containing six or more strains and constituting 307 (64·6%) of the strains studied, were defined at the 77·5% *S*-level (Table 1, Fig. 2). Details of the test results for these clusters are given in Table 4; character states which were most representative of and consistent within each cluster are marked by an asterisk. These data and those for minor clusters (Tables 5 and 6) and single member clusters (Table 7) summarize the test results of all clusters defined. They should serve as a reference source for taxonomists and workers studying other aspects of streptomycetes. It is, however, generally inadvisable to use the data in this form to attempt to identify streptomycetes, as diagnostic properties cannot be accurately selected by eye. The data for the major clusters have been further analysed and used to construct a probabilistic identification scheme (Williams *et al.*, 1983).

Cluster 1 (*Streptomyces albidoflavus*) was the largest, containing 59 strains with different specific epithets and 12 unnamed strains. The cluster could be divided into three sub-clusters, A to C, at the 81% *S*-level (Table 1). The 20 strains of sub-cluster 1A formed hooked/retinaculi-aperti (RA) or straight/rectiflexibiles (RF) chains of smooth, yellow or white spores and were melanin-negative. It contained *S. albidoflavus* ISP 5455, *S. coelicolor* ISP 5233, together with *S. felleus* ISP 5130 and *S. limosus* ISP 5131, which had a similarity of over 97%. Sub-cluster 1B comprised 38 strains which were similar in morphology and pigmentation to those in sub-cluster 1A. It included *S. griseus* ISP 5236 which was over 90% similar to *S. bikiniensis* ISP 5235, *S. fluorescens* ISP 5203 and '*S. ornatus*' ISP 5307. The 13 strains in sub-cluster 1C produced grey, smooth spores and were melanin-negative. They included *S. olivaceus* ISP 5072, together with *S. griseolus* ISP 5067 and *S. halstedii* ISP 5068, which fused at the 95% *S*-level.

Cluster 3 (*Streptomyces atroolivaceus*) contained nine strains including *S. olivaceus* G7, '*S. scabies*' ISP 5078 and *S. atroolivaceus* ISP 5137, the latter sharing over 92% similarity with *S. olivoviridis* ISP 5211. All strains had smooth, grey or white spores in RF chains and were melanin-negative on peptone/yeast/iron agar (Difco) (PYIA). They had many properties in common with strains in cluster 1.

Cluster 5 (*Streptomyces exofoliatus*) contained 18 strains which produced RF chains of smooth, red or grey spores and shared many properties with those in clusters 1 and 3. Half of the strains, including *S. cinereoruber* ISP 5012 and *S. umbrinus* ISP 5278, produced distinctive red-brown substrate pigments and melanin. The remainder, including *S. exofoliatus* ISP 5060 and *S. filamentosus* ISP 5022, did not produce these pigments.

The eight strains in cluster 6 (*Streptomyces violaceus*) shared many properties with cluster 5. They included *S. cellostaticus* ISP 5189, *S. violaceus* ISP 5082 and *S. violascens* ISP 5183, which united at the 91% *S*-level and produced an unusual violet spore mass.

Cluster 10 (*Streptomyces fulvissimus*) was defined above the 80% *S*-level and contained three strains of *S. spectabilis* among its nine members. Eight strains produced a red-orange, pH-sensitive substrate mycelial pigment.

The third largest phenon was cluster 12 (*Streptomyces rochei*) which contained 26 strains. Most had spiral (S) or RA chains of grey spores and did not produce melanin or other substrate pigments. About half of the strains had smooth spores, while the rest showed a range of ornamentation as exemplified by *S. calvus* ISP 5010 with hairy spores, *S. griseorubens* ISP 5160 with spiny spores and '*S. pulcher*' ISP 5566 with warty spores.

Cluster 15 (*Streptomyces chromofuscus*) contained nine strains including *Chainia flava* ISP 5270 and *C. minutisclerotia* ISP 5301, which produced sclerotia, unlike the streptomycetes.

Cluster 16 (*Streptomyces albus*) was defined at the 84% *S*-level and contained six strains, which included the type species of the genus, *S. albus* ISP 5313. *Streptomyces almquistii* ISP 5447 and *S. flocculus* ISP 5327 fused at the 91% *S*-level. Strains produced smooth, white spores in S chains and lacked substrate pigmentation.

Table 3. *Distribution of positive characters to cluster-groups defined at the 70·1% similarity level (S_{SM})*

For major cluster-groups, values are the percentage of strains with positive character states and, for minor cluster-groups, the number of strains with positive character states.

	Major cluster-groups						Minor cluster-groups				
	Streptomyces spp.	*Streptomyces rimosus*	*Streptomyces* spp.	*Actinomadura* spp./'*Nocardia*' *mediterranea*	*Streptoverticillium* spp./*Kitasatoa* spp./ *Streptomyces lavendulae*	'*Streptomyces viridoflavus*'/*Actinomadura pelletieri*/Acidophilic isolates	*Microellobosporia violacea*/ *Streptomyces massasporeus*	*Streptomyces fradiae*	*Streptomyces cyaneogriseus*/ *Streptomyces lateritius*	*Nocardia* spp.	'*Nocardia capreola*'
Cluster groups ...	A·	B	C	E	F	J	D	G	H	I	225
Cluster numbers ...	1–41	42	43–47	48–54	55–67	70–73	—	68	—	69	—
Number of strains ...	340	7	16	25	60	15	2	3	2	3	1
Morphology and pigmentation:											
1. Presence of spores (aerial mycelium)	98	90	100	56	97	53	2	3	2	3	1
Spore chain morphology:											
2. Rectiflexibiles	39	13	6	28	40	27	1	0	0	3	0
3. Retinaculiaperti	16	0	31	12	5	13	0	3	0	0	0
4. Spirales	47	63	69	16	17	13	1	1	2	0	1
5. Verticillati	0	0	0	0	43	0	0	0	0	0	0
Spore chain ornamentation:											
6. Smooth	74	88	81	48	95	27	2	3	2	2	1
7. Warty	2	0	6	4	0	6	0	0	0	0	0
8. Spiny	15	0	0	0	0	7	0	0	0	0	0
9. Hairy	4	0	13	0	2	13	0	0	0	1	0
10. Rugose	2	0	0	4	0	0	0	0	0	0	0
11. Production of aerial spore mass	90	75	88	28	95	47	1	3	2	3	1
Colour of aerial spore mass:											
12. Red	15	0	0	4	53	7	0	3	1	2	1
13. Yellow	18	25	13	4	10	7	0	0	0	0	0
14. Grey	38	0	56	0	18	7	0	0	1	1	0
15. Green	4	0	0	0	5	7	0	0	0	0	0
16. Blue	5	13	0	4	2	7	0	0	0	0	0
17. Violet	1	0	13	0	0	0	1	0	0	0	0
18. White	10	38	6	16	7	13	0	0	0	0	0
19. No distinctive substrate mycelial pigments	80	100	75	64	95	80	0	3	1	1	1
Pigmentation of substrate mycelium:											
20. Red/orange	12	0	19	36	5	20	0	0	1	1	0
21. Green	4	0	6	0	0	0	0	0	0	1	0
22. Blue	2	0	0	0	0	0	0	0	0	0	0
23. Violet	2	0	0	0	0	0	2	0	0	0	0
24. Production of diffusible pigments	25	0	50	4	18	0	2	0	1	0	1
Pigmentation of diffusible pigments:											
25. Red/orange	7	0	25	0	5	0	0	0	1	0	0
26. Yellow/brown	13	0	25	4	13	0	0	0	0	0	1
27. Green	2	0	0	0	0	0	0	0	0	0	0
28. Blue	1	0	0	0	0	0	0	0	0	0	0
29. Violet	2	0	0	0	0	0	2	0	0	0	0
30. Sensitivity of substrate pigment to pH	19	13	31	12	5	13	1	0	1	0	0
31. Sensitivity of diffusible pigment to pH	12	0	25	0	2	0	1	0	1	0	0

Table 3 (*continued*)

Cluster groups ...	A	B	C	E	F	J	D	G	H	I	225
Cluster numbers ...	1–41	42	43–47	48–54	55–67	70–73	—	68	—	69	—
Number of strains ...	340	7	16	25	60	15	2	3	2	3	1
32. Melanin production on peptone/yeast/iron agar	34	0	13	8	70	0	1	0	2	0	0
33. Melanin production on tyrosine agar	31	0	19	4	45	0	1	0	2	0	0
34. Fragmentation of mycelium	2	0	0	44	0	7	0	0	0	1	1
35. Sclerotia formation	4	0	0	0	0	0	0	0	0	0	0
66. Sporulation on substrate mycelium	4	0	0	0	0	0	1	0	0	0	0
Antimicrobial activity against:											
54. *Bacillus subtilis* NCIB 3610	34	100	13	20	70	20	2	2	2	0	0
55. *Pseudomonas fluorescens* NCIB 9046	3	38	0	0	18	0	0	1	1	0	0
56. *Escherichia coli* NCIB 9132	3	25	0	0	28	7	1	2	1	0	0
57. *Micrococcus luteus* NCIB 196	37	88	25	40	85	7	0	3	2	0	0
58. *Candida albicans* CBS 562	17	63	0	4	48	0	2	0	0	0	0
58. *Saccharomyces cerevisiae* CBS 1171	19	75	6	0	47	0	2	1	1	0	0
60. *Streptomyces murinus* ISP 5091	44	100	31	28	77	27	1	2	2	0	0
61. *Aspergillus niger* LIV 131	22	100	6	8	67	7	0	1	1	0	0
Enzyme activity:											
47. Lecithinase } on egg-yolk medium	18	75	6	8	82	0	2	2	1	1	0
48. Proteolysis } on egg-yolk medium	86	63	94	48	95	47	0	3	1	1	0
49. Lipolysis } on egg-yolk medium	74	88	75	36	60	33	0	3	1	1	0
50. Pectin hydrolysis	45	13	19	16	5	0	2	2	1	1	0
51. Chitin hydrolysis	27	63	19	20	27	0	2	2	1	1	0
52. Nitrate reduction	47	75	13	48	35	33	1	1	2	2	0
53. Hydrogen sulphide production	85	25	81	83	53	47	2	1	1	3	0
62. Hippurate hydrolysis	29	63	31	12	2	0	0	0	0	0	0
63. β-Lactamase production on YPG agar	60	88	44	40	65	20	2	3	0	0	1
64. β-Lactamase production on Beecham's FS agar	59	63	44	40	67	20	2	3	0	0	1
65. Production of *Klebsiella* β-lactamase inhibitor	6	0	0	0	0	7	0	0	0	0	0
Degradation of:											
67. Hypoxanthine	95	88	94	68	92	67	2	1	2	0	1
68. Guanine	87	63	81	72	73	53	0	2	2	0	1
69. Elastin	64	100	31	56	82	47	0	2	1	0	1
70. L-Tyrosine	94	100	81	84	97	80	2	1	2	2	1
71. Adenine	91	88	94	32	35	33	2	3	2	3	0
72. Xanthine	77	75	63	20	62	0	1	0	2	0	1
73. DNA	87	75	69	64	78	60	2	3	0	3	1
74. RNA	95	88	100	84	93	47	2	3	1	2	1
75. Tween 80	98	100	94	84	98	80	0	3	2	2	1
76. Starch	75	50	75	44	58	60	1	2	2	1	1
77. Xylan	22	50	13	4	5	7	0	3	0	0	1
78. Casein	99	100	94	88	98	100	2	3	2	2	1
79. Testosterone	86	88	75	72	80	40	2	1	1	1	1
80. Urea	84	100	81	56	65	13	1	1	1	3	1
81. Allantoin	53	75	63	44	40	0	0	0	0	2	0
82. Gelatin	99	100	100	96	98	87	1	3	2	1	1
83. Aesculin	99	75	94	100	82	80	2	3	2	3	1
84. Arbutin	82	63	50	52	35	67	2	3	2	1	0
Resistance to antibiotics ($\mu g\ ml^{-1}$):											
85. Gentamicin (100)	1	63	6	40	13	27	0	0	1	0	1
86. Neomycin (50)	6	88	19	76	62	47	0	1	1	1	1
87. Streptomycin (100)	11	88	19	36	13	40	0	0	0	0	0
88. Tobramycin (50)	2	63	6	64	25	33	0	0	1	0	1
89. Rifampicin (50)	59	88	75	80	28	27	2	0	1	2	1
90. Cephaloridine (100)	97	88	100	100	98	80	1	2	2	3	1
91. Vancomycin (50)	4	0	6	40	15	7	0	0	1	0	0
92. Dimethylchlortetracycline (500)	7	50	13	4	22	0	1	0	0	0	0
93. Oleandomycin (100)	44	63	44	68	30	20	1	0	2	2	0
94. Lincomycin (100)	91	100	88	100	88	80	2	3	2	2	1
95. Penicillin G (10 i.u.)	68	88	69	68	62	27	1	1	1	0	0

Table 3 (*continued*)

Cluster groups ...	A	B	C	E	F	J	D	G	H	I	225
Cluster numbers ...	1–41	42	43–47	48–54	55–67	70–73	—	68	—	69	—
Number of strains ...	340	7	16	25	60	15	2	3	2	3	1
Growth at:											
96. 4 °C	40	13	13	4	28	27	0	0	1	2	0
97. 10 °C	81	88	75	56	80	53	2	2	2	3	0
98. 37 °C	77	75	100	80	78	47	2	3	2	0	1
99. 45 °C	33	38	44	28	28	13	1	3	1	0	1
100. pH 4·3	4	0	13	12	10	27	0	0	1	0	0
Growth in the presence of (%, w/v):											
101. Sodium chloride (4)	93	100	94	56	73	13	2	3	2	3	0
102. Sodium chloride (7)	49	88	63	20	17	7	0	0	1	0	0
103. Sodium chloride (10)	19	38	38	8	0	0	0	0	0	0	0
104. Sodium chloride (13)	4	0	13	0	0	0	0	0	0	0	0
105. Sodium azide (0·01)	42	63	44	8	17	0	0	1	0	0	0
106. Sodium azide (0·02)	18	13	25	0	3	0	0	0	0	0	0
107. Phenylethanol (0·1)	94	100	100	84	82	33	2	3	2	3	1
108. Phenylethanol (0·3)	9	0	13	4	2	0	0	1	0	0	0
109. Phenol (0·1)	70	63	50	32	30	7	2	1	1	1	0
110. Potassium tellurite (0·001)	70	75	81	56	37	40	1	3	0	3	1
111. Potassium tellurite (0·01)	18	13	0	32	3	13	0	0	0	2	1
112. Thallous acetate (0·001)	45	25	19	32	12	33	1	0	2	3	0
113. Thallous acetate (0·01)	5	0	0	0	0	0	0	0	0	1	0
114. Crystal violet (0·0001)	73	100	75	72	75	33	1	2	2	3	0
Growth on sole nitrogen source (0·1%, w/v):											
36. DL-α-Amino-n-butyric acid	41	0	0	8	28	7	0	0	1	3	1
37. Potassium nitrate	89	88	81	40	88	40	2	3	2	3	1
38. L-Cysteine	58	25	44	20	87	7	0	0	0	3	0
39. L-Valine	45	50	31	20	47	40	1	0	0	2	1
40. L-Threonine	80	88	44	16	78	60	2	2	2	2	1
41. L-Serine	89	88	75	36	78	67	0	3	2	3	1
42. L-Phenylalanine	58	88	38	28	53	53	0	2	0	1	1
43. L-Methionine	20	13	6	8	12	13	2	1	0	2	1
44. L-Histidine	70	88	75	40	55	53	2	0	1	3	1
45. L-Arginine	90	75	94	60	98	80	0	1	2	3	1
46. L-Hydroxyproline	32	25	6	16	37	40	1	0	1	0	1
Growth on sole carbon source (1·0%, w/v):											
115. L-Arabinose	87	75	50	100	35	13	2	2	2	2	1
116. Sucrose	53	0	6	88	37	7	2	0	0	2	0
117. D-Xylose	84	88	13	76	22	27	2	3	2	2	1
118. *meso*-Inositol	65	100	25	72	50	13	2	0	0	1	1
119. Mannitol	88	100	50	96	15	27	2	0	0	2	1
120. D-Fructose	89	88	56	96	82	33	2	0	2	2	0
121. L-Rhamnose	70	0	13	76	17	27	2	2	2	2	0
122. Raffinose	57	88	19	56	22	27	2	1	0	2	1
123. D-Melezitose	53	50	19	56	40	7	2	1	0	1	0
124. D-Mannose	99	100	75	100	93	27	2	1	2	3	1
125. D-Lactose	90	88	25	72	23	7	2	2	0	1	0
126. Inulin	28	13	0	28	8	0	2	0	0	0	0
127. Adonitol	43	100	6	60	12	20	2	0	0	1	0
128. Salicin	85	88	6	72	42	20	1	2	2	1	0
129. Trehalose	95	100	63	100	85	53	1	3	2	2	0
130. D-Melibiose	68	100	38	84	13	7	2	1	0	1	1
131. Dextran	41	13	0	28	2	0	0	0	1	0	1
132. D-Galactose	89	100	63	92	53	40	1	1	0	2	1
133. Cellobiose	96	100	50	92	50	33	1	1	1	3	1
134. Xylitol	18	88	6	16	8	7	1	0	0	1	0
135. Sodium acetate (0·1%, w/v)	60	75	6	80	58	20	1	0	0	1	0
136. Sodium citrate (0·1%, w/v)	74	100	19	80	65	40	1	2	0	1	0
137. Sodium malonate (0·1%, w/v)	25	0	0	20	3	7	0	0	0	1	0
138. Sodium propionate (0·1%, w/v)	77	100	13	72	53	27	0	2	0	2	0
139. Sodium pyruvate (0·1%, w/v)	59	88	13	64	55	13	0	1	1	1	1

The six strains in cluster 17 (*Streptomyces griseoviridis*) all produced smooth, red spores in S chains, were melanin-negative and formed a yellow-brown diffusible pigment.

The second largest phenon, cluster 18 (*Streptomyces cyaneus*) contained 38 strains. These included *Actinosporangium violaceum* MAV and *S. collinus*, which had a similarity of 88%; *S. iakyrus* ISP 5482 and *S. luteogriseus* ISP 5483 fused at the 91% *S*-level. This cluster contained many of the strains with blue, spiny spores, such as *S. chartreusis* ISP 5085, and ten organisms, including *S. bellus* ISP 5185, that produced red-orange, pH-sensitive pigments.

Cluster 19 (*Streptomyces diastaticus*) contained 20 strains, which included two species of *Microellobosporia*. *Microellobosporia cinerea* M301 joined *S. lincolnensis* ISP 5355 at the 86% *S*-level, while *M. flavea* M315 and *S. vastus* ISP 5309 had a similarity of 90%.

Cluster 20 (*Streptomyces olivaceoviridis*) consisted of three *Elytrosporangium* and four *Streptomyces* species which united at the 81% *S*-level to form this phenon. The elytrosporangias bore spores on both their substrate and aerial mycelia.

Cluster 21 (*Streptomyces griseoruber*) contained nine strains, including two labelled *S. griseoruber* (ISP 5275 and ISP 5281). *Actinopycnidium caeruleum* E35 joined with '*S. caesius*' ISP 5419 at the 93% *S*-level. Most strains produced smooth, grey spores in S chains and formed distinctive pH-sensitive, diffusible pigments which were red, blue or violet.

The 11 strains in cluster 29 (*Streptomyces lydicus*) included *S. lydicus* ISP 5461 and '*S. saraceticus*' ISP 5241, which united at the 89% *S*-level. The strains typically formed grey, smooth spores in S chains and lacked distinctive substrate pigments.

Cluster 32 (*Streptomyces violaceoniger*) contained six strains all of which produced rugose spores formed in tight spirals and which autolysed to a black slime. The latter is a well-known property of *S. hygroscopicus* ISP 5578 which fell into this cluster.

Five of the six strains in cluster 37 (*Streptomyces griseoflavus*) united at or above the 89% *S*-level; *S. griseoflavus* ISP 5456 joined the cluster at 79%. Most strains formed ornamented, green spores in RA chains and were melanin-negative, as typified by *S. hirsutus* ISP 5095 and *S. prasinus* ISP 5099.

The final major phenon in cluster-group A was cluster 40 (*Streptomyces phaeochromogenes*), which contained six strains including *Chainia antibiotica* ISP 5269, *C. nigra* ISP 5302, *C. purpurogena* ISP 5271 and *C. violens* ISP 5597. The chainias united at or above the 82% *S*-level and were joined by *S. phaeochromogenes* ISP 5073 and '*S. verne*' ISP 5079 at 79%. Unlike the streptomycetes, all the chainias formed sclerotia.

The only phenon in cluster-group B was cluster 42 (*Streptomyces rimosus*). This contained seven strains including *S. anandii* ISP 5535 and *S. chrestomyceticus* ISP 5545, which shared a similarity of 94%. Members of this cluster produced RF or S chains of smooth, white or yellow spores and lacked substrate pigments.

Cluster 50 (*Actinomadura* spp.) was a major phenon in cluster-group E and contained five *Actinomadura* strains together with *Microtetraspora glauca* E63. *Actinomadura pusilla* A3 and *A. roseoviolacea* A2 joined at the 82% *S*-level; *A. verrucosospora* A4 shared a similarity of over 82% with *A. madurae* A16 and A17. Not all strains formed spores and those that did produced insufficient for determination of spore mass colour. Half of the orgnaisms formed a red substrate pigment but none produced melanin. The actinomaduras showed less enzymic activity and ability to degrade substrates than the streptomycetes.

The largest phenon in cluster-group E was cluster 53 ('*Nocardia*' *mediterranea*) which contained five strains received as either '*N.*' *mediterranea* or '*S. mediterranei*', two as '*S. tolypophorus*' and a single *Streptomyces* strain. Fragmentation of mycelium occurred in all strains, but only half produced spores. Most formed a red-orange substrate mycelial pigment.

Cluster 55 (*Streptoverticillium griseocarneum*) was one of the two major phena in cluster-group F. It comprised seven *Streptoverticillium* strains and two received as '*Streptomyces*'. Of the latter, '*S. paucisporogenes*' ISP 5315 joined *Stv. septatum* ISP 5577 at the 87% *S*-level and '*S. tropicalensis*' ISP 5520 fused with *Stv. cinnamoneum* ISP 5005 at 84%. All strains produced verticillate (V) chains of smooth, red, yellow or grey spores and most were melanin-positive.

The other major phenon in cluster-group F was cluster 61 (*Streptomyces lavendulae*) which contained 12 strains. They produced RF chains of smooth, red spores and were melanin-positive.

Tests for the distinctiveness of major clusters. Most of the major clusters showed little overlap, though cluster 1 (*S. albidoflavus*) was a notable exception. The index of overlap, V_G, exceeded 20% between *S. albidoflavus* and clusters 6 (*S. violaceus*) and 42 (*S. rimosus*), the corresponding value for the latter two taxa being 0·02%. Clusters 5 (*S. exfoliatus*), 15 (*S. chromofuscus*), 17 (*S. griseoviridis*) and 53 ('*N.*' *mediterranea*) showed V_G values within the range 7 to 14% with *S. albidoflavus*, but these clusters were distinct from one another. Clusters 5 (*S. exfoliatus*) and 6 (*S. violaceus*) were closely related in both the S_{SM} and S_J analyses (Figs 2 and 3) and gave a V_G index of just over 6%. Clusters 18 (*S. cyaneus*) and 19 (*S. diastaticus*) each showed some overlap with cluster 40 (*S. phaeochromogenes*) but not with one another. *Streptomyces cyaneus* also overlapped with cluster 21 (*S. griseoruber*).

Composition and characteristics of minor clusters. One hundred and forty strains (29·5%) representing eight genera were recovered in the 51 minor clusters defined at the 77·5% *S*-level (Table 1); they were assigned to cluster-groups A, C, E, F, G, I and J. Five of the clusters contained five strains, three contained four and the rest included only two or three strains. Test results of these clusters are given in Tables 5 and 6. The detailed affinities of 15 of them can be seen in Fig. 2.

Cluster-group A. This contained 21 of the minor phena. Cluster 2 contained '*Streptoverticillium*' *olivoverticillatum* ISP 5250, which produced RF spore chains and fused with major cluster 1 (*S. albidoflavus*) at the 77% *S*-level. *Nocardiopsis dassonvillei* A14 and A15 formed cluster 4 at the 92% *S*-level and united with major cluster 3 (*S. atroolivaceus*) at 77%. The *Nocardopsis* strains formed RF chains of smooth, white spores with fragmentation of their substrate mycelia.

Cluster 7 included '*S. roseus*' ISP 5076, which united at 77% with '*S. alni*' ISP 5557 and '*Kitasatoa antimyceticus*' M673. The latter two strains formed cluster 8 and were negative for over half of the unit characters.

Streptomyces californicus ISP 5058 together with two other strains formed cluster 9 at the 87% *S*-level, while *S. prunicolor* ISP 5335 and a soil isolate comprised cluster 11 at 83%. Both clusters fused with major cluster 10 (*S. fulvissimus*) at 74%.

Cluster 13 was composed of *S. cellulosae* ISP 5362 and *S. griseocarnatus* ISP 5274 which joined at the 81% *S*-level, whereas cluster 14 comprised *S. aureofaciens* ISP 5127 and *S. roseofulvus* ISP 5172 which united at 79%. The two clusters shared their closest similarities to the *S. rochei* and *S. chromofuscus* strains of major clusters 12 and 15, respectively.

Chainia poonensis ISP 5596 and *C. rosea* ISP 5303 formed cluster 22 at the 81% *S*-level and showed their highest affinity to the *S. griseoruber* strains of major cluster 21. The two strains produced sclerotia.

Minor clusters 23 to 26 were more closely related to one another than to any other of the phena. Cluster 23 contained five strains including *S. microflavus* ISP 5313. *Streptomyces flaveolus* ISP 5061 and two other strains comprised cluster 24. *Streptomyces canus* ISP 5017 and '*S. ostreogriseus*' ISP 5511 formed cluster 25 at the 81% *S*-level, and *S. graminofaciens* ISP 5559 and '*S. pristinaespiralis*' ISP 5558 united at 89% to form cluster 26.

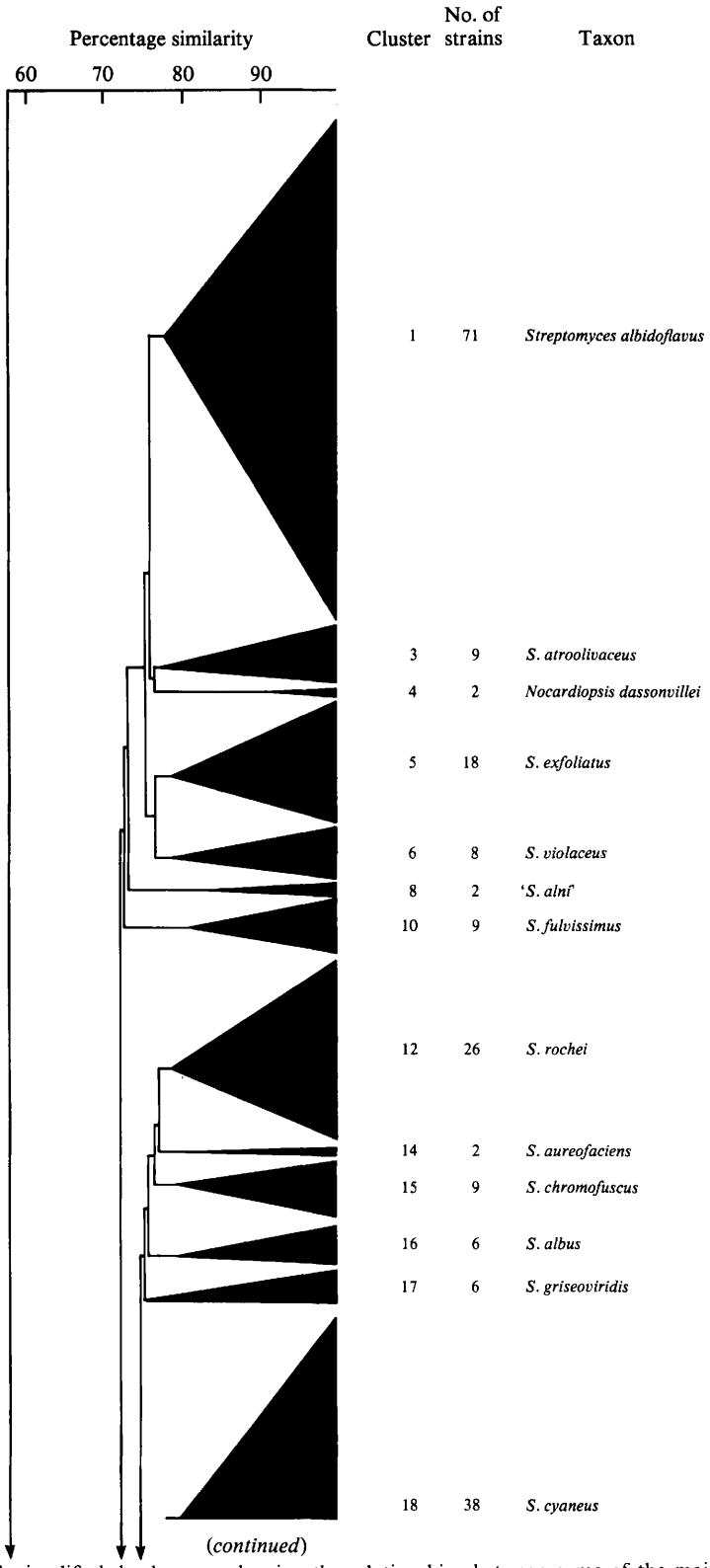
Clusters 27 and 28 each contained two strains and joined at the 74% *S*-level. *Streptomyces viridochromogenes* ISP 5110 and '*S. viridis*' ISP 5381 formed cluster 27 at the 82% *S*-level, while *S. flavoviridis* ISP 5153 and *S. glaucescens* ISP 5155 united at the 84% *S*-level to give cluster 28.

Cluster 30 contained four strains, including *S. filipinensis* ISP 5112, which joined cluster 31 at the 76% *S*-level. The latter phenon encompassed *S. antibioticus* ISP 5234 and five other strains.

Phena 33 and 34 encompassed five and three strains, respectively, and fused at the 73% *S*-level; the former included '*S. chromogenus*' ISP 5384 and the latter *S. nogalater* ISP 5546.

Clusters 35 and 36 united at the 76% *S*-level and showed their closest similarity with the *S. griseoflavus* strains in major cluster 37. *Streptomyces chattanoogensis* ISP 5002 and *S. nodosus* ISP 5109 joined at the 81% *S*-level, whereas the three thermophilic strains '*S. thermoflavus*' ISP 5574, *S. thermonitrificans* ISP 5579 and *S. thermovulgaris* ISP 5444 formed a homogeneous phenon at the 85% *S*-level. The strains in clusters 38 and 39 also shared an affinity with *S. griseoflavus* (cluster 37) and joined it at the 75% *S*-level.

The last minor phenon in cluster-group A comprised *Chainia ochracea* ISP 5594 and *Saccharopolyspora hirsuta* N745, which formed cluster 41 at the 79% *S*-level. The former



(*continued*)

Fig. 2. A simplified dendrogram showing the relationships between some of the major and minor clusters defined at the 77·5% similarity level in the S_{SM}/UPGMA analysis.

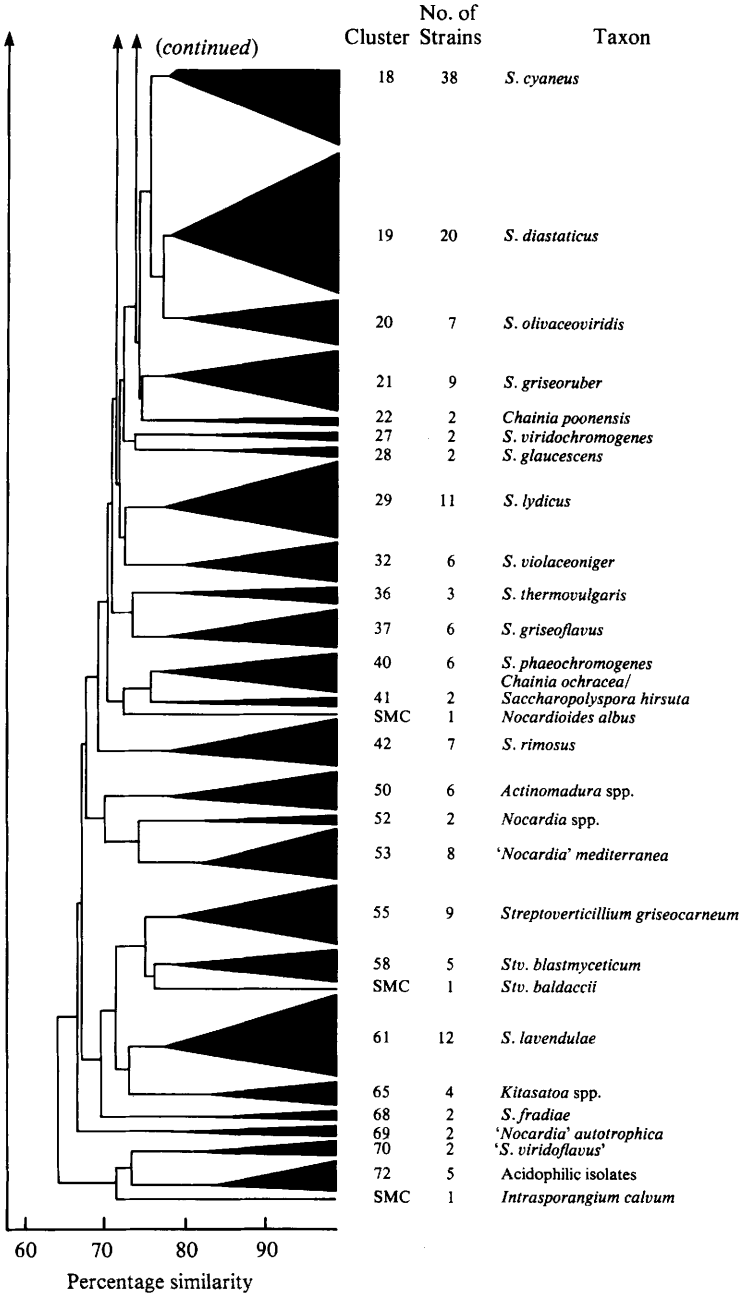


Fig. 2 (*continued*)

produced sclerotia, while the latter had spore chains and fragmentation of substrate mycelium.

Cluster-group C. The five minor clusters in this group united at the 72% *S*-level. The phena were divided into two, clusters 43 to 45 fusing at 74% and clusters 46 and 47 joining just below that point. Phena 43 and 44 each contained three strains; the former included *S. griseoluteus* ISP 5392, and the latter '*S. karnatakensis*' ISP 5345 and *S. pactum* ISP 5530 which joined at the 96% *S*-level. *Streptomyces aurantiacus* ISP 5412 was one of the three strains in cluster 45. Cluster 46 contained '*S. paraguayensis*' ISP 5567 and *S. varsoviensis* ISP 5346 which joined at the 79% *S*-level, whereas the two strains in cluster 47, '*S. cattleya*' G1 and *S. tubercidicus* ISP 5261, fused at 82%.

Table 4. *Distribution of positive characters to major clusters defined at the 77·5% similarity level (S_{SM})*

Values are the percentage of strains with positive character states. Character states which are most representative of and consistent within each cluster are marked with an asterisk.

	Streptomyces albidoflavus	*Streptomyces atroolivaceus*	*Streptomyces exfoliatus*	*Streptomyces violaceus*	*Streptomyces fulvissimus*	*Streptomyces rochei*	*Streptomyces chromofuscus*	*Streptomyces albus*	*Streptomyces griseoviridis*	*Streptomyces cyaneus*	*Streptomyces diastaticus*	*Streptomyces olivaceoviridis*	*Streptomyces griseoruber*	*Streptomyces lydicus*	*Streptomyces violaceoniger*	*Streptomyces griseoflavus*	*Streptomyces phaeochromogenes*	*Streptomyces rimosus*	*Actinomadura* spp.	'*Nocardia*' *mediterranea*	*Streptoverticillium griseocarneum*	*Streptomyces lavendulae*
Cluster number ...	1	3	5	6	10	12	15	16	17	18	19	20	21	29	32	37	40	42	50	53	55	61
Number of strains ...	71	9	18	8	9	26	9	6	6	38	20	7	9	11	6	6	6	7	6	8	9	12
Morphology and pigmentation:																						
1. Presence of spores (aerial mycelium)	99	100	100	100	100	96	100	100	100	100	100	100	100	100	100	100	100	86	67	50	100	100
Spore chain morphology:																						
2. Rectiflexibiles	83	100*	100*	38	67	4	22	0	0	5	42	0	0	0	0	0	0	14	17	50	0	92*
3. Retinaculiaperti	13	11	0	13	22	40	0	0	0	13	11	14	0	0	0	100*	33	0	33	0	0	0
4. Spirales	9	0	0	50	22	64	78	100	100	82	58	86	100	100	100	0	67	57	17	0	0	17
5. Verticillati	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100*	0
Spore chain ornamentation:																						
6. Smooth	100	100	100	63	100	48	67	100	100	41	100	100	89	64	0	0	100	86	50	50	100	100
7. Warty	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	17	0	0	0
8. Spiny	0	0	0	38	0	24	22	0	0	59	0	0	11	27	0	67	0	0	0	0	0	0
9. Hairy	0	0	0	0	0	16	11	0	0	0	0	0	0	9	0	33	0	0	0	0	0	0
10. Rugose	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100*	0	0	0	0	0	0	0
11. Production of aerial spore mass	92	100	94	100	89	92	78	100	100	97	90	100	89	100	100	100	17	71	17	25	100	100
Colour of aerial spore mass:																						
12. Red	3	0	42	13	75	8	0	0	100*	32	18	14	13	9	0	17	0	0	0	0	67	83
13. Yellow	63	0	12	38	0	4	43	17	0	3	0	14	0	0	0	0	0	29	0	13	22	0
14. Grey	20	67	41	13	13	83	43	0	0	32	53	71	88	91	100*	0	0	0	0	0	11	8
15. Green	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	83*	0	0	0	0	0	0
16. Blue	0	0	0	0	0	0	0	0	0	34	0	0	0	0	0	0	0	0	17	0	0	8
17. Violet	0	0	0	38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18. White	14	33	6	0	13	0	14	83	0	0	29	0	0	0	0	0	17	43	0	13	0	0
19. No distinctive substrate mycelial pigments	96	56	89	100	11	89	100	100	100	69	79	71	0*	100	100	67	83	100	50	25	100	100

Cluster number ...	1	3	5	6	10	12	15	16	17	18	19	20	21	29	32	37	40	42	50	53	55	61
Number of strains ...	71	9	18	8	9	26	9	6	6	38	20	7	9	11	6	6	6	7	6	8	9	12
Pigmentation of substrate mycelium:																						
20. Red/orange	1	0	11	0	89*	8	0	0	0	21	16	0	67	0	0	0	0	0	50	75	0	0
21. Green	3	44	0	0	0	4	0	0	0	3	5	29	0	0	0	17	17	0	0	0	0	0
22. Blue	0	0	0	0	0	0	0	0	0	3	0	0	23	0	0	17	0	0	0	0	0	0
23. Violet	0	0	0	0	0	0	0	0	0	5	0	0	11	0	0	0	0	0	0	0	0	0
24. Production of diffusible pigments	13	11	39	0	33	4	11	0	100*	33	10	29	100*	0	0	0	50	0	0	13	0	0
Pigmentation of diffusible pigments:																						
25. Red/orange	1	0	6	0	33	0	0	0	0	15	0	0	67	0	0	0	0	0	0	0	0	0
26. Yellow/brown	11	0	28	0	0	4	11	0	100*	13	5	29	0	0	0	0	33	0	0	13	0	0
27. Green	1	11	0	0	0	0	0	0	0	0	5	0	0	0	0	0	17	0	0	0	0	0
28. Blue	0	0	0	0	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0
29. Violet	0	0	6	0	0	0	0	0	0	5	0	0	11	0	0	0	0	0	0	0	0	0
30. Sensitivity of substrate pigment to pH	1	11	11	13	89*	23	11	0	17	31	16	0	100*	0	0	17	33	0	33	0	11	0
31. Sensitivity of diffusible pigment to pH	1	11	17	0	33	0	0	0	17	23	0	0	100*	0	0	0	33	0	0	0	0	0
32. Melanin production on peptone/yeast/iron agar	7	0	61	88	67	4	33	0	0	97*	47	14	22	0	0	17	17	0	0	0	78	100*
33. Melanin production on tyrosine agar	14	11	61	100*	0	0*	22	0	17	85	47	14	22	0	0	17	33	0	0	0	44	92
34. Fragmentation of mycelium	1	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	100*	0	0
35. Sclerotia formation	1	0	0	0	0	4	22	0	0	3	0	0	0	0	0	0	67	0	0	0	0	0
66. Sporulation on substrate mycelium	0	0	0	0	0	4	22	0	0	0	11	43	0	0	0	0	67	0	0	0	0	0
Antimicrobial activity against:																						
54. *Bacillus subtilis* NCIB 3610	28	33	56	50	78	35	11	17	100	44	21	0	0	73	67	17	17	100	0	38	78	92
55. *Pseudomonas fluorescens* NCIB 9046	4	0	17	0	0	8	0	0	0	0	0	0	0	0	0	0	0	29	0	0	44	50
56. *Escherichia coli* NCIB 9132	9	0	0	13	0	8	0	0	0	3	0	0	0	0	0	0	0	29	0	0	96*	83
57. *Micrococcus luteus* NCIB 196	39	33	44	38	89	35	11	17	100	33	21	0	0	100	100	17	17	86	17	88	89	83
58. *Candida albicans* CBS 562	34	11	0	0	11	19	0	0	33	3	0	0	0	27	17	0	0	57	0	0	100*	67
58. *Saccharomyces cerevisiae* CBS 1171	32	0	0	0	22	15	0	0	33	5	0	29	0	27	50	0	17	86	0	0	89	67
60. *Streptomyces murinus* ISP 5091	39	33	39	88	100	39	22	17	80	62	5	0	22	100	50	67	0	100	17	13	89	100
61. *Aspergillus niger* LIV 131	32	11	6	25	22	27	0	17	33	10	11	0	0	100	33	0	0	100	0	0	100	75
Enzyme activity:																						
47. Lecithinase } on egg-yolk medium	6	11	50	75	44	4	11	0	50	10	0	0	0	64	0	0	0	86	0	0	100*	100*
48. Proteolysis } on egg-yolk medium	90	100	83	100	100	85	89	33	100	77	79	100	89	73	83	100	100	71	0*	100	100	100
49. Lipolysis } on egg-yolk medium	99	100	94	63	100	73	89	100	83	49	26	86	89	18	100	100	83	100	0*	63	89	33
50. Pectin hydrolysis	45	89	61	13	0	42	22	0	67	56	68	14	100*	0	50	100*	50	14	0	13	0	8
51. Chitin hydrolysis	52	33	61	0	0	23	11	17	50	0	10	29	0	9	83	50	17	71	33	25	56	25
52. Nitrate reduction	55	89	83	100	0	27	22	0	33	36	47	14	89	9	83	83	17	86	83	38	0	50
53. Hydrogen sulphide production	92	100	89	63	67	92	89	83	100	90	79	100	100	0*	100	100	83	14	83	100	22	42
62. Hippurate hydrolysis	23	13	44	88	44	9	13	0	67	3	28	50	56	30	67	67	83	71	0	38	0	0
63. β-Lactamase production on YPG agar	69	50	89	75	40	36	25	50	33	87	90	43	22	40	40	33	83	86	100*	0*	44	92
64. β-Lactamase production on Beecham's FS agar	66	50	89	75	20	40	13	33	67	80	79	57	33	50	60	17	50	57	100*	0*	56	92
65. Production of *Klebsiella* β-lactamase inhibitor	3	22	6	0	20	8	38	0	0	0	0	0	11	0	0	0	17	0	0	0	0	0

Table 4 (*continued*)

Cluster number ...	1	3	5	6	10	12	15	16	17	18	19	20	21	29	32	37	40	42	50	53	55	61
Number of strains ...	71	9	18	8	9	26	9	6	6	38	20	7	9	11	6	6	6	7	6	8	9	12
Degradation of:																						
67. Hypoxanthine	99	100	100	100	100	100	67	100	100	100	100	86	100	100	83	50	100	100	50	88	100	100
68. Guanine	97	100	100	75	100	92	78	100	100	97	63	100	78	91	17	50	100	43	50	100	89	100
69. Elastin	90	89	89	88	67	50	67	50	50	41	37	57	44	36	83	17	100	100	17	88	78	92
70. L-Tyrosine	99	67	94	100	100	92	89	67	67	97	95	100	100	100	100	67	100	100	100	100	100	100
71. Adenine	94	89	94	100	100	69	100	33	100	100	95	86	100	100	100	100	100	86	17	0*	11	8
72. Xanthine	97	100	94	88	100	96	22	83	83	80	53	29	78	82	0*	0*	100	86	0*	0*	56	83
73. DNA	96	67	78	38	100	92	67	100	67	95	68	100	67	82	100	100	67	71	67	100	100	75
74. RNA	99	100	100	100	100	92	89	100	83	92	84	100	56	91	100	100	100	86	33	100	100	100
75. Tween 80	100	100	100	100	100	100	100	100	100	97	95	71	100	100	100	100	100	100	50	100	100	100
76. Starch	85	56	89	100	67	73	89	33	33	49	84	100	67	100	100	100	100	57	50	0*	89	8*
77. Xylan	4	33	50	13	0	12	33	0	0	46	16	14	44	0	33	17	50	57	0	13	0	8
78. Casein	100	100	100	100	100	100	100	100	100	100	100	100	100	91	100	100	100	100	100	100	100	100
79. Testosterone	86	67	94	100	100	85	89	100	100	87	94	100	78	100	100	83	83	100	100	75	78	92
80. Urea	86	100	94	100	100	85	67	100	100	95	100	43	89	73	100	67	83	100	0*	100	44	75
81. Allantoin	83	44	83	75	78	50	33	100*	17	54	32	14	78	18	50	0	100*	86	0	63	0	50
82. Gelatin	100	89	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	92
83. Aesculin	100	100	100	100	100	100	100	100	100	97	100	100	100	100	100	100	100	71	100	100	56	100
84. Arbutin	99	100	100	100	67	96	100	100	100	54	53	0*	100	100	100	50	67	71	50	13	0*	92
Resistance to antibiotics ($\mu g\ ml^{-1}$):																						
85. Gentamicin (100)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	71	83	13	11	8
86. Neomycin (50)	1	11	11	25	89	8	0	0	0	0	0	0	0	18	0	0	0	100*	33	88	100*	50
87. Streptomycin (100)	24	0	0	0	67	4	0	0	0	3	0	0	0	27	33	0	0	100*	50	25	33	8
88. Tobramycin (50)	0	0	0	13	44	4	0	0	0	0	0	0	0	0	0	0	0	71	17	88	11	8
89. Rifampicin (50)	54	89	11	100	100	89	33	100	83	46	68	86	78	9*	83	50	50	100	100	100	33	33
90. Cephaloridine (100)	100	100	100	100	100	100	100	100	100	87	95	100	100	100	100	100	100	100	100	100	100	100
91. Vancomycin (50)	0	0	0	0	33	0	0	0	0	0	5	0	67	0	0	0	0	0	0	38	22	0
92. Dimethylchlortetracycline (500)	0	0	6	0	56	4	0	67	33	3	5	0	0	0	17	0	33	57	0	0	44	0
93. Oleandomycin (100)	86	78	44	13	100*	46	0	83	17	13	26	0	0	9	50	83	33	71	67	50	44	8
94. Lincomycin (100)	97	89	94	50	100	100	67	100	100	82	90	100	100	91	100	100	100	100	100	100	100	92
95. Penicillin G (10 i.u.)	83	100	44	100	100	92	44	100	100	64	47	14	78	91	17	83	33	100	83	38	78	58
Growth at:																						
96. 4 °C	82	100*	44	75	0	15	11	17	50	10	68	0	33	0	0	50	17	14	0	13	11	42
97. 10 °C	100	100	100	100	100	81	22	0	100	77	100	43	89	64	0	83	83	86	0	100	78	100
98. 37 °C	54	11	61	75	78	100	89	100	100	92	74	100	100	55	67	100	83	86	100	100	89	67
99. 45 °C	7	0	17	0	22	77	67	100*	67	41	16	86	0	0	50	0	67	43	67	0	11	17
100. pH 4·3	1	0	0	0	0	4	0	0	50	3	0	29	0	27	0	0	0	0	0	13	0	8
Growth in the presence of (%, *w/v*):																						
101. Sodium chloride (4)	97	89	83	100	67	96	100	100	100	82	100	100	100	100	67	100	100	100	17	50	67	83
102. Sodium chloride (7)	83	44	22	38	22	92	44	100*	83	18	32	29	78	55	0	33	83	100*	17	0	0	0
103. Sodium chloride (10)	27	11	6	25	0	42	11	83	0	3	5	0	56	18	0	0	83	43	0	0	0	0
104. Sodium chloride (13)	10	0	0	0	0	0	0	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
105. Sodium azide (0·01)	56	0	23	63	0	62	56	100*	100*	15	5	57	11	18	50	33	67	71	0	0	11	0
106. Sodium azide (0·02)	23	0	6	25	0	35	0	83	33	0	5	43	0	0	33	0	17	14	0	0	0	0

Cluster number ...	1	3	5	6	10	12	15	16	17	18	19	20	21	29	32	37	40	42	50	53	55	61
Number of strains ...	71	9	18	8	9	26	9	6	6	38	20	7	9	11	6	6	6	7	6	8	9	12
107. Phenylethanol (0·1)	99	67	94	100	78	100	100	100	100	92	95	100	100	91	83	100	100	100	83	100	78	75
108. Phenylethanol (0·3)	10	0	0	13	0	19	0	0	50	0	0	0	0	0	0	17	0	0	0	0	0	0
109. Phenol (0·1)	90	56	72	100	44	96	22	17	83	64	95	86	89	9	0	100	100	71	17	0	0	58
110. Potassium tellurite (0·001)	92	56	83	100	56	73	67	50	100	46	74	57	78	55	17	100	100	71	50	75	22	42
111. Potassium tellurite (0·01)	51	0	22	25	0	12	11	0	17	0	0	0	0	9	0	17	33	14	0	75	0	0
112. Thallous acetate (0·001)	92*	11	67	63	22	54	54	0	50	13	21	14	33	46	0	50	33	14	17	38	11	17
113. Thallous acetate (0·01)	18	0	6	0	0	4	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
114. Crystal violet (0·0001)	87	33	61	88	100	73	33	67	100	69	79	50	89	82	100	0*	83	100	67	75	78	67
Growth on sole nitrogen source (0·1%, w/v):																						
36. DL-α-Amino-n-butyric acid	54	33	61	88	89	12	67	0	0	31	32	57	33	9	100*	17	67	0	0	0	11	42
37. Potassium nitrate	80	100	100	88	89	96	100	17	83	100	90	86	100	100	100	100	100	100	0*	88	89	92
38. L-Cysteine	65	56	50	38	44	50	67	0*	83	72	79	100	78	46	33	17	17	29	67	13	33	33
39. L-Valine	44	0	50	50	100	15	33	17	17	69	74	86	56	27	33	0	100	57	0	50	89	17
40. L-Threonine	72	78	100	88	100	77	100	67	83	92	90	100	100	55	83	67	83	86	17	25	100	50
41. L-Serine	83	89	83	88	100	85	100	100	83	100	95	100	89	64	100	100	100	86	50	50	100	42
42. L-Phenylalanine	64	89	83	100	89	46	11	17	33	67	16	71	33	100	67	17	83	86	0*	50	78	42
43. L-Methionine	27	0	17	38	0	8	44	0	0	39	11	29	11	9	17	33	33	14	0	13	11	8
44. L-Histidine	65	78	78	25	100	77	78	100	83	85	68	100	100	36	100	17	83	100	33	88	100	8*
45. L-Arginine	85	100	100	88	100	89	89	100	100	100	95	100	100	100	83	100	83	86	67	100	100	92
46. L-Hydroxyproline	23	11	89	88	78	8	0	67	17	28	21	0	22	55	83	17	67	29	0	38	78	42
Growth on sole carbon source (1·0%, w/v):																						
115. L-Arabinose	85	78	89	88	100	100	100	67	83	90	95	86	100	55	100	100	100	71	100	100	22	58
116. Sucrose	31	11	28	38	34	81	33	33	17	92	74	86	44	73	33	83	83	0*	100*	100*	33	50
117. D-Xylose	93	67	89	100	100	96	100	67	83	90	90	43	89	27	67	100	100	86	67	88	11	33
118. *meso*-Inositol	37	0*	6	63	100	96	89	33	67	92	84	57	100	91	67	83	100	100	33	100	78	25
119. Mannitol	94	89	0*	38	100	100	100	100	100	95	90	100	100	91	100	100	100	100	100	100	11	8*
120. D-Fructose	93	78	56	100	100	89	100	67	100	90	100	86	100	91	83	83	100	86	100	88	100	75
121. L-Rhamnose	62	78	61	38	22	96	67	17	83	92	95	100	100	18	83	83	100	0*	100	88	33	17
122. Raffinose	17	22	33	63	89	69	22	33	50	100	84	100	100	82	83	33	100	86	33	63	11	8*
123. D-Melezitose	61	0*	22	50	44	81	22	67	33	72	26	29	56	82	83	67	100*	57	33	63	56	33
124. D-Mannose	100	100	100	100	100	100	100	100	100	100	100	100	100	91	100	100	100	100	100	100	100	92
125. D-Lactose	96	89	94	88	89	96	100	100	100	97	90	86	89	73	100	83	100	86	50	100	22	25
126. Inulin	10	0	33	0	11	27	0	0	17	80	63	43	11	18	33	17	100*	0	17	13	11	0
127. Adonitol	51	11	0*	13	89	35	22	100	67	82	16	14	22	82	67	0*	100	100	100	13	11	8*
128. Salicin	97	44	100	100	67	92	78	100	100	90	90	57	78	64	83	67	100	86	67	88	11	75
129. Trehalose	99	89	50	88	100	100	100	100	100	98	100	100	100	100	100	100	100	100	100	100	89	50
130. D-Melibiose	39	11	28	75	89	96	44	50	33	98	95	100	78	82	83	67	83	100	67	100	33	17
131. Dextran	59	22	6	13	22	89	78	0	17	59	16	14	44	0	17	50	50	14	0	0	11	0
132. D-Galactose	97	89	94	100	100	96	100	67	83	100	80	71	89	82	83	100	100	100	100	100	22	50
133. Cellobiose	100	89	100	100	100	100	100	100	100	95	100	100	100	73	100	100	100	100	100	100	0*	83
134. Xylitol	13	0	0	0	11	46	0	0	0	21	16	29	0	55	17	0	100*	86	17	0	22	0
135. Sodium acetate (0·1%, w/v)	59	33	78	88	89	85	78	50	50	85	42	14	67	55	50	33	17	71	67	100*	56	58
136. Sodium citrate (0·1%, w/v)	80	44	72	88	100	89	89	100	83	80	68	71	89	82	67	0*	33	100	100	100	67	67
137. Sodium malonate (0·1%, w/v)	20	0	22	13	11	65	22	17	17	44	32	0	33	27	33	0	17	0	17	13	0	0
138. Sodium propionate (0·1%, w/v)	89	44	83	88	100	89	100	83	83	82	90	86	78	46	50	50	67	100	67	100	78	67
139. Sodium pyruvate (0·1%, w/v)	83	44	72	100	67	92	78	100	67	64	68	57	67	64	67	33	33	86	33	100	56	58

Cluster-group E. This group contained five minor phena. Clusters 48, 49 and 51 were loosely associated with the *Actinomadura* strains in the major cluster 50, whereas, in contrast, clusters 52 and 54 showed their closest affinity with the major cluster 53 which contained '*Nocardia*' *mediterranea* and '*S. tolypophorus*'. Cluster 48 contained '*S. pyridomyceticus*' ISP 5024 and an isolate from fodder, which fused at the 79% *S*-level. Two other fodder isolates united at the 82% *S*-level to give cluster 49, whereas two acidophilic isolates, MR10 and MR19, formed cluster 51 at a similarity of 89%.

Cluster 54 contained three strains including '*S. alboflavus*' ISP 5045, while *Nocardia asteroides* N317 and '*Nocardia*' *orientalis* ISP 5040 were loosely associated at the 77·5% *S*-level to give cluster 52.

Cluster-group F. This group contained 11 minor clusters which were associated with one or other of its two major clusters. Thus, clusters 56 to 59 were closely related with *Stv. cinnamoneum* (cluster 55), whereas 60, and 62 to 67 showed a greater affinity to *S. lavendulae* (cluster 61). Cluster 56 comprised four strains, which included *Stv. netropsis* ISP 5259 and *S. avidinii* ISP 5526; *Stv. hiroshimense* ISP 5037 and *Stv. rectiverticillatum* ISP 5436 formed cluster 57 at the 81% *S*-level. The five strains in cluster 58 included *Stv. blastmyceticum* ISP 5029 and '*S. caespitosus*' ISP 5603, while cluster 59 contained *Stv. biverticillatum* M635, '*S. aspergilloides*' ISP 5565 and '*S. morookaensis*' ISP 5503.

Cluster 60 contained '*Stv. griseostramineus*' ISP 5161 and '*Stv. kurssanovii*' ISP 5162 which joined at the 81% *S*-level, whereas clusters 62, 63 and 64 each consisted of three strains including *S. luridus* ISP 5081, *S. xanthochromogenes* ISP 5111 and *S. bikiniensis* ISP 5581, respectively. Cluster 65 contained four of the five *Kitasatoa* strains, while *S. avellaneus* ISP 5554 and *S. psammoticus* ISP 5341 united at the 82% *S*-level to give cluster 67.

Cluster-groups G, I and J. Cluster-group G contained a single minor cluster (68) formed by the fusion of *S. fradiae* ISP 5063 and *S. roseolilacinus* ISP 5173 at the 81% *S*-level.

Cluster-group I consisted of '*Nocardia*' *autotrophica* ISP 5011 and '*Nocardia*' *salmonicida* ISP 5472 which formed cluster 69 at the 77·5% *S*-level.

Cluster-group J contained four minor clusters encompassing strains which showed a high proportion of negative test results. Cluster 70 contained two strains, which included '*S. somaliensis*' A28 and '*S. viridoflavus*' ISP 5237, and cluster 71 was formed by the fusion of *S. clavuligerus* G2 and '*S. jumonjinensis*' G4 at the 81% *S*-level. *Actinomadura pelletieri* A19 and A20 united at the 88% *S*-level to give cluster 73 and the five remaining acidophilic soil isolates formed cluster 72 at 85%.

Single member clusters. Twenty-eight strains (5·9%) were not assigned to any of the major or minor clusters. Test reactions of these are given in Table 7.

Cluster-groups A and F contained the largest number of unclustered strains. The former included six *Streptomyces* strains and *Nocardioides albus* N950, which was recovered on the periphery of this cluster-group. Cluster-group F contained *Stv. baldacci* M636, the type species of the genus *Streptoverticillium*, and three other strains in this group which also produced verticillate spore chains. *Intrasporangium calvum* 1C was closest to '*S. luteofluorescens*' and *Actinomadura helvata* A5 showed a close affinity to the actinomaduras in cluster 50. *Microellobosporia violacea* M297 was closest to *S. massasporeus* ISP 5035. The remaining eleven *Streptomyces* strains were distributed among cluster-groups B, C, D, G, H, I and J.

Clustering of strains by the S_J coefficient with the UPGMA algorithm

The S_J coefficient excludes negative matches in the determination of overall similarity, thereby reducing the similarity levels at which phena are recognized. It is a useful adjunct to the S_{SM} coefficient as it can alter groupings constructed primarily on the basis of negative matches. With streptomycetes this has particular relevance for qualitative multistate characters, such as spore features, where it provides a back-up for results obtained when NC scores were included in the calculation of the S_{SM} coefficient. In the present study, it was decided, after inspection of the dendrograms, to define cluster-groups at the 50% *S*-level and clusters at 63%.

The changes of strains between cluster-groups and clusters resulting from use of the S_J coefficient are detailed in Table 8 and the main clusters obtained are illustrated in Fig. 3. As far

Table 5. *Distribution of positive characters to minor clusters defined at the 77·5% similarity level (S_{SM}); cluster-groups A and C*
Values are the number of strains with positive character states.

	Cluster-group A																								Cluster-group C				
	'Streptoverticillium' olivoverticillatum	*Nocardiopsis dassonvillei*	*'Streptomyces roseus'*	*'Streptomyces alni'*	*Streptomyces californicus*	*Streptomyces prunicolor*	*Streptomyces cellulosae*	*Streptomyces aureofaciens*	*'Chainia' poonensis*	*Streptomyces microflavus*	*Streptomyces flaveolus*	*Streptomyces canus*	*Streptomyces graminofaciens*	*Streptomyces viridochromogenes*	*Streptomyces glaucescens*	*Streptomyces filipinensis*	*Streptomyces antibioticus*	*'Streptomyces chromogenus'*	*Streptomyces nogalater*	*Streptomyces chattanoogensis*	*Streptomyces thermovulgaris*	*Streptomyces prasinosporus*	*Streptomyces longisporoflavus*	*Chainia ochracea*	*Streptomyces griseoluteus*	*Streptomyces pactum*	*Streptomyces aurantiacus*	*Streptomyces varsoviensis*	*Streptomyces tubercidicus*
Cluster number ...	2	4	7	8	9	11	13	14	22	23	24	25	26	27	28	30	31	33	34	35	36	38	39	41	43	44	45	46	47
Number of strains ...	3	2	3	2	3	2	2	2	2	5	3	2	2	2	2	4	5	5	3	2	3	3	3	2	3	3	3	2	2
Morphology and pigmentation:																													
1. Presence of spores (aerial mycelium)	3	2	3	2	3	2	2	2	2	5	3	2	2	2	2	4	5	5	3	2	2	3	2	2	3	3	3	2	2
Spore chain morphology:																													
2. Rectiflexibiles	3	2	3	2	3	2	0	2	0	1	0	0	0	0	0	0	1	4	0	0	1	0	0	0	0	0	0	0	0
3. Retinaculiaperti	0	0	0	0	0	0	1	1	0	3	1	1	0	0	0	0	1	0	3	1	0	0	0	1	3	0	0	0	0
4. Spirales	0	0	0	0	0	0	1	0	2	2	3	1	2	2	2	4	3	2	0	2	1	3	2	1	0	3	3	2	2
5. Verticillati	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spore chain ornamentation:																													
6. Smooth	3	2	3	2	3	2	1	2	2	5	2	1	0	0	0	0	4	5	3	1	1	0	1	1	3	0	3	2	2
7. Warty	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0
8. Spiny	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0	4	0	0	0	1	0	1	0	0	0	0	0	0	0
9. Hairy	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	1	0	0	0	0	1	0	1	0	2	0	0	0
10. Rugose	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
11. Production of aerial spore mass	1	2	3	1	3	2	2	2	1	5	3	2	2	2	2	4	5	5	3	2	1	3	0	1	3	3	2	2	2
Colour of aerial spore mass:																													
12. Red	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0
13. Yellow	0	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
14. Grey	1	0	0	0	1	0	1	1	0	4	1	2	2	0	1	2	5	2	3	0	0	1	0	0	3	3	2	0	0
15. Green	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
16. Blue	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
17. Violet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2

Table 5 (*continued*)

Cluster number ...	2	4	7	8	9	11	13	14	22	23	24	25	26	27	28	30	31	33	34	35	36	38	39	41	43	44	45	46	47
Number of strains ...	3	2	3	2	3	2	2	2	2	5	3	2	2	2	2	4	5	5	3	2	3	3	3	2	3	3	3	2	2
18. White	0	2	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0
19. No distinctive substrate mycelial pigments	3	2	3	2	0	0	0	2	0	4	3	2	2	1	0	3	5	5	3	2	3	3	1	2	2	3	0	2	2
Pigmentation of substrate mycelium:																													
20. Red/orange	0	0	0	0	0	2	2	0	2	1	0	0	2	0	2	1	0	0	0	0	0	0	0	0	0	0	3	0	0
21. Green	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
22. Blue	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23. Violet	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24. Production of diffusible pigments	0	0	0	2	3	2	2	0	1	1	2	0	0	1	1	2	0	5	3	1	0	0	0	0	0	3	3	0	0
Pigmentation of diffusible pigments:																													
25. Red/orange	0	0	0	0	0	1	2	0	1	1	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	3	0	0
26. Yellow/brown	0	0	0	2	0	1	0	0	0	0	3	0	0	0	0	0	0	5	3	2	0	0	0	0	0	3	0	0	0
27. Green	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
28. Blue	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29. Violet	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30. Sensitivity of substrate pigment to pH	0	0	0	0	3	2	2	0	2	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	3	0	2
31. Sensitivity of diffusible pigment to pH	0	0	0	0	3	2	2	0	2	0	0	0	0	1	0	2	0	0	1	0	0	0	0	0	0	0	3	0	0
32. Melanin production on peptone/yeast/iron agar	0	0	0	0	0	0	0	0	0	4	0	1	0	2	2	4	4	5	2	0	0	2	1	0	1	0	1	0	0
33. Melanin production on tyrosine agar	0	0	0	0	0	0	0	0	0	4	0	2	0	1	2	4	3	5	1	0	0	1	0	0	1	0	1	0	0
34. Fragmentation of mycelium	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
35. Sclerotia formation	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
66. Sporulation on substrate mycelium	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Antimicrobial activity against:																													
54. *Bacillus subtilis* NCIB 3610	1	0	3	0	2	1	1	0	0	4	0	0	2	0	1	2	2	1	0	0	0	0	0	0	0	1	0	0	0
55. *Pseudomonas fluorescens* NCIB 9046	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56. *Escherichia coli* NCIB 9132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57. *Micrococcus luteus* NCIB 196	1	0	1	0	1	0	1	2	0	5	0	1	2	0	2	4	1	0	0	0	0	1	0	0	1	1	0	0	0
58. *Candida albicans* CBS 562	1	0	3	1	0	0	0	0	0	0	0	0	0	0	0	4	5	5	0	2	0	0	0	0	0	0	0	0	0
58. *Saccharomyces cerevisiae* CBS 1171	2	0	3	0	0	0	0	0	1	0	0	0	0	0	0	4	5	5	1	2	1	0	0	0	0	0	1	0	0
60. *Streptomyces murinus* ISP 5091	0	0	3	0	2	0	1	1	0	5	2	1	2	0	2	4	4	2	2	0	0	1	0	0	0	2	0	1	0
61. *Aspergillus niger* LIV 131	2	0	0	0	1	0	1	0	1	0	0	0	0	0	1	4	4	0	0	2	0	1	0	0	0	1	0	0	0
Enzyme activity:																													
47. Lecithinase } on egg-yolk medium	2	0	0	1	0	0	0	0	0	3	3	0	2	1	0	3	2	3	0	0	1	0	0	0	0	0	0	0	1
48. Proteolysis } on egg-yolk medium	2	2	3	2	3	1	2	2	2	5	3	2	2	2	0	4	4	4	3	2	3	3	2	1	3	3	3	2	1
49. Lipolysis } on egg-yolk medium	2	2	0	2	3	0	2	2	2	2	1	0	2	2	2	2	0	3	3	1	3	2	3	1	1	3	2	2	1
50. Pectin hydrolysis	1	0	0	0	0	0	0	1	1	5	0	2	1	0	2	0	2	1	3	0	0	3	3	1	0	0	0	0	0

Cluster number ...	2	4	7	8	9	11	13	14	22	23	24	25	26	27	28	30	31	33	34	35	36	38	39	41	43	44	45	46	47
Number of strains ...	3	2	3	2	3	2	2	2	2	5	3	2	2	2	2	4	5	5	3	2	3	3	3	2	3	3	3	2	2
51. Chitin hydrolysis	1	0	2	1	0	0	0	0	2	3	0	0	1	0	0	0	1	0	3	0	0	1	0	0	0	2	0	0	0
52. Nitrate reduction	0	2	3	1	2	0	0	1	1	0	0	0	0	0	0	0	4	4	1	1	2	2	3	0	0	0	0	1	0
53. Hydrogen sulphide production	3	2	2	2	3	2	2	2	1	5	3	2	2	2	2	3	0	5	3	1	3	3	3	2	3	3	3	1	0
62. Hippurate hydrolysis	0	2	1	0	0	0	0	0	0	2	0	2	2	0	0	0	2	0	3	1	0	0	0	2	0	0	1	2	1
63. β-Lactamase production on YPG agar	2	1	0	2	0	1	2	2	2	0	1	2	2	1	2	2	4	3	2	0	1	0	3	2	2	0	3	1	0
64. β-Lactamase production on Beecham's FS agar	1	2	0	2	1	2	1	2	2	0	1	2	2	2	2	4	5	2	3	0	1	1	2	2	2	0	3	1	0
65. Production of *Klebsiella* β-lactamase inhibitor	1	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Degradation of:																													
67. Hypoxanthine	3	2	3	2	3	2	2	2	2	5	3	2	2	2	2	4	4	5	2	0	0	3	3	2	3	3	2	2	2
68. Guanine	3	2	3	2	3	2	2	2	1	5	2	2	2	2	1	4	5	4	2	0	0	0	0	2	3	3	1	2	2
69. Elastin	2	2	3	2	3	0	0	2	1	3	3	2	2	1	0	2	0	2	3	1	2	0	2	1	0	2	0	0	0
70. L-Tyrosine	3	2	3	2	3	2	2	2	1	5	3	2	2	2	1	4	5	5	1	2	3	2	3	2	3	3	2	1	2
71. Adenine	3	2	3	2	3	2	0	2	2	5	3	1	0	0	2	4	5	5	3	2	2	3	3	2	3	2	3	2	2
72. Xanthine	3	2	1	1	3	2	2	2	1	3	3	2	2	2	1	4	4	1	2	0	1	0	1	2	1	3	0	1	2
73. DNA	3	2	3	2	3	1	2	1	2	5	2	1	2	2	2	4	4	5	3	2	3	3	2	2	2	3	3	1	0
74. RNA	3	2	3	2	3	2	2	1	2	5	3	2	2	2	2	3	5	5	3	2	3	3	3	2	3	3	3	2	2
75. Tween 80	3	2	3	2	3	2	2	2	2	5	3	1	2	2	2	3	5	5	3	2	3	3	3	2	3	3	3	2	1
76. Starch	3	0	3	2	2	2	2	2	2	4	2	2	2	0	1	3	2	3	0	2	3	2	2	2	3	3	3	0	1
77. Xylan	2	0	0	0	0	0	0	1	0	1	2	2	2	0	2	0	1	0	3	0	0	0	2	2	0	0	0	0	1
78. Casein	3	2	3	2	3	2	2	2	2	5	3	2	2	2	2	4	5	4	3	2	3	3	3	2	3	3	2	2	2
79. Testosterone	3	0	3	0	3	2	0	2	2	2	2	2	2	1	2	3	4	1	3	2	3	2	3	2	3	1	1	2	2
80. Urea	2	0	3	2	3	2	1	2	2	5	3	2	0	1	1	0	3	4	1	2	0	2	3	2	2	3	2	2	1
81. Allantoin	1	0	3	2	3	0	0	0	2	0	2	0	0	0	0	0	0	0	2	1	0	0	1	1	2	2	2	1	1
82. Gelatin	3	2	3	2	3	2	2	2	2	5	3	2	2	2	2	4	5	5	3	2	3	3	2	2	3	3	3	2	2
83. Aesculin	3	2	3	2	3	2	2	2	2	5	3	2	2	2	2	4	5	5	2	2	3	3	3	2	3	3	3	2	2
84. Arbutin	2	2	3	2	3	0	2	1	2	5	1	1	1	2	2	3	5	3	2	2	3	2	2	0	1	1	2	1	2
Resistance to antibiotics ($\mu g\ ml^{-1}$):																													
85. Gentamicin (100)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0
86. Neomycin (50)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	1	0
87. Streptomycin (100)	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	2	0
88. Tobramycin (50)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0
89. Rifampicin (50)	3	0	0	0	3	2	2	1	0	5	2	1	1	2	2	3	1	4	2	0	0	1	3	2	2	0	2	2	1
90. Cephaloridine (100)	3	2	3	2	3	2	2	2	2	5	3	2	2	2	2	4	5	5	2	2	2	3	3	2	3	3	3	2	2
91. Vancomycin (50)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	1	0
92. Dimethylchlortetracycline (500)	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	2	0	0	0	2	0
93. Oleandomycin (100)	3	2	1	0	2	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1	0	1	1	0	3	1	2	0
94. Lincomycin (100)	3	2	3	1	3	2	2	1	2	4	3	2	2	2	2	1	4	5	3	2	1	3	3	2	2	2	3	2	2
95. Penicillin G (10 i.u.)	3	0	3	2	2	0	2	1	2	1	1	2	1	0	0	1	2	4	1	1	0	1	2	2	1	1	2	2	2

Table 5 (*continued*)

Cluster number ...	2	4	7	8	9	11	13	14	22	23	24	25	26	27	28	30	31	33	34	35	36	38	39	41	43	44	45	46	47
Number of strains ...	3	2	3	2	3	2	2	2	2	5	3	2	2	2	2	4	5	5	3	2	3	3	3	2	3	3	3	2	2
Growth at:																													
96. 4 °C	3	0	1	0	3	2	0	1	0	0	1	2	2	0	0	0	1	1	0	0	0	0	2	0	0	0	1	0	0
97. 10 °C	3	0	2	2	3	2	2	2	0	3	1	2	2	2	2	2	4	5	2	1	0	1	2	2	3	1	2	2	2
98. 37 °C	3	1	1	1	1	0	2	2	2	5	3	2	2	2	2	3	4	5	3	2	3	3	3	2	3	3	3	2	2
99. 45 °C	1	0	0	0	0	0	2	1	2	3	3	1	0	2	2	1	4	0	3	0	3	2	0	1	1	3	2	0	1
100. pH 4·3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1
Growth in the presence of (%, *w/v*):																													
101. Sodium chloride (4)	3	2	3	2	3	2	2	1	2	5	1	2	2	2	2	4	4	4	3	2	3	3	2	2	3	3	3	2	1
102. Sodium chloride (7)	3	2	0	0	3	0	1	0	0	0	0	1	2	0	1	0	1	1	0	1	0	0	2	2	2	1	1	2	1
103. Sodium chloride (10)	2	2	0	0	2	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	1	0	0	2	0
104. Sodium chloride (13)	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
105. Sodium azide (0·01)	3	0	0	1	3	0	2	2	0	3	2	0	0	2	1	3	3	0	1	2	3	1	2	2	3	1	0	0	0
106. Sodium azide (0·02)	2	0	0	0	3	0	0	0	0	2	0	0	0	0	0	1	2	0	0	2	2	0	1	1	1	0	0	0	0
107. Phenylethanol (0·1)	3	2	2	1	3	1	2	2	2	4	3	2	2	2	2	4	5	4	3	2	3	2	2	2	3	3	3	2	2
108. Phenylethanol (0·3)	3	0	0	0	2	0	0	0	0	2	0	0	0	0	0	0	1	0	0	1	2	0	0	0	1	0	0	1	0
109. Phenol (0·1)	2	0	2	1	3	0	2	2	2	5	2	1	2	2	1	2	4	3	1	2	3	3	1	2	3	1	1	1	0
110. Potassium tellurite (0·001)	3	0	0	0	3	1	2	2	2	4	0	0	2	1	2	0	3	1	2	2	3	1	2	2	3	3	1	2	2
111. Potassium tellurite (0·01)	2	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
112. Thallous acetate (0·001)	3	0	3	1	0	0	1	1	0	0	1	0	2	0	0	0	2	0	1	2	2	0	0	0	2	0	1	0	0
113. Thallous acetate (0·01)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114. Crystal violet (0·0001)	3	1	0	2	3	2	1	1	1	4	1	0	2	1	1	3	4	5	3	2	2	3	2	2	3	3	2	1	1
Growth on sole nitrogen source (0·1%, *w/v*):																													
36. DL-α-Amino-n-butyric acid	2	0	1	1	1	2	0	1	1	3	2	0	1	0	0	1	1	5	0	0	0	0	0	2	0	0	0	0	0
37. Potassium nitrate	2	2	0	1	3	2	2	0	2	5	3	2	2	2	2	4	4	5	3	1	1	3	3	2	3	3	3	0	2
38. L-Cysteine	1	0	1	2	2	2	1	0	1	3	1	0	2	2	2	4	4	5	1	0	0	0	1	2	3	0	2	0	1
39. L-Valine	0	1	3	0	2	1	0	0	1	2	1	0	0	0	0	4	3	2	2	0	0	0	0	2	1	1	1	0	0
40. L-Threonine	1	1	3	2	3	2	1	0	1	4	2	2	2	2	2	4	3	4	3	0	1	1	2	2	1	3	1	1	1
41. L-Serine	3	2	3	2	3	2	0	1	2	5	2	2	1	2	2	4	4	3	3	2	0	3	3	2	3	3	1	2	2
42. L-Phenylalanine	2	1	3	2	3	2	0	0	0	5	3	1	2	0	1	2	2	3	2	2	0	0	1	2	2	2	0	0	1
43. L-Methionine	0	0	1	1	0	0	0	0	0	1	2	0	0	1	0	0	1	0	0	1	0	0	0	2	0	0	0	0	1
44. L-Histidine	3	0	3	1	3	1	1	0	2	2	1	0	0	1	1	4	5	1	3	2	1	0	0	1	3	3	1	2	2
45. L-Arginine	3	2	3	2	3	1	1	1	2	5	2	0	2	1	2	4	3	5	2	2	3	1	2	2	3	3	3	2	2
46. L-Hydroxyproline	3	0	0	1	3	0	0	0	0	1	1	0	0	1	0	3	2	2	0	0	0	0	1	1	0	0	0	0	1

Cluster number ...	2	4	7	8	9	11	13	14	22	23	24	25	26	27	28	30	31	33	34	35	36	38	39	41	43	44	45	46	47
Number of strains ...	3	2	3	2	3	2	2	2	2	5	3	2	2	2	2	4	5	5	3	2	3	3	3	2	3	3	3	2	2
Growth on sole carbon source (1·0%, w/v):																													
115. L-Arabinose	3	1	0	1	1	2	2	2	2	5	3	2	1	2	2	4	5	5	3	1	3	0	3	1	0	1	3	0	2
116. Sucrose	2	2	0	0	0	1	1	2	0	5	3	2	2	0	2	2	4	0	0	2	1	1	2	2	0	0	0	0	0
117. D-Xylose	3	0	1	0	2	2	2	2	2	5	3	2	2	1	0	2	5	3	2	2	3	2	3	1	1	0	0	0	0
118. *meso*-Inositol	2	0	0	2	2	1	2	2	2	2	3	0	1	2	1	3	4	3	2	2	1	2	3	2	1	1	1	0	1
119. Mannitol	3	2	0	2	2	2	2	2	2	5	3	1	2	2	2	3	4	3	3	2	3	3	3	2	3	1	0	1	0
120. D-Fructose	3	2	1	2	3	2	2	2	2	4	3	1	2	0	2	4	4	4	2	2	3	3	3	2	3	1	3	0	0
121. L-Rhamnose	2	2	1	0	1	2	1	2	1	4	3	0	2	2	2	1	3	1	2	0	0	3	3	2	0	0	1	0	0
122. Raffinose	1	2	0	0	0	2	0	1	0	5	2	1	2	2	0	4	3	4	1	1	3	1	3	2	0	0	1	0	1
123. D-Melezitose	3	0	0	0	2	1	1	2	1	2	2	1	0	0	0	3	4	0	0	1	3	0	1	2	1	0	0	1	0
124. D-Mannose	3	2	3	1	3	1	2	1	2	5	3	2	2	2	2	4	5	5	3	2	3	2	3	2	3	2	1	2	2
125. D-Lactose	3	2	1	1	1	1	2	2	2	5	2	1	1	1	2	4	5	5	3	2	2	2	3	0	0	2	0	0	1
126. Inulin	1	0	0	0	0	0	0	1	2	3	0	1	1	0	1	1	0	0	1	0	0	1	0	2	0	0	0	0	0
127. Adonitol	3	0	0	0	3	0	1	1	0	0	1	2	0	0	0	4	1	0	0	0	0	1	0	2	0	0	0	0	0
128. Salicin	3	2	3	1	3	2	2	2	2	3	3	2	2	2	0	3	5	2	0	1	1	2	2	1	0	0	0	1	0
129. Trehalose	3	2	0	0	3	2	2	2	2	5	3	2	2	2	2	4	5	5	3	2	3	3	3	2	3	3	3	0	0
130. D-Melibiose	2	2	1	1	2	2	2	2	2	2	3	2	1	2	0	3	5	5	3	2	3	2	2	2	1	0	0	1	2
131. Dextran	3	0	0	0	3	1	2	1	0	0	1	0	0	1	1	0	0	1	2	0	0	0	2	0	0	0	0	0	0
132. D-Galactose	3	1	1	0	3	2	2	2	1	4	3	1	1	1	0	4	4	5	3	2	3	1	3	2	2	3	1	1	2
133. Cellobiose	3	2	1	1	3	1	2	2	1	4	3	1	1	2	2	4	5	5	3	2	3	2	3	2	2	3	2	1	0
134. Xylitol	2	0	0	0	0	1	0	0	2	2	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1
135. Sodium acetate (0·1%, w/v)	2	0	2	0	3	1	2	2	2	2	2	0	0	1	0	1	4	2	2	0	2	1	0	1	1	0	0	0	0
136. Sodium citrate (0·1%, w/v)	3	2	0	0	3	1	2	2	1	3	2	1	2	1	1	2	5	4	2	0	2	2	1	1	2	0	0	0	1
137. Sodium malonate (0·1%, w/v)	3	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
138. Sodium propionate (0·1%, w/v)	3	2	3	1	2	1	2	2	2	1	0	0	2	1	0	1	5	3	2	2	1	0	0	1	1	0	0	0	0
139. Sodium pyruvate (0·1%, w/v)	3	1	2	0	2	2	2	2	1	1	0	0	2	1	0	3	4	2	2	0	3	1	0	1	1	0	0	1	0

Table 6. *Distribution of positive characters to minor clusters at the 77·5% similarity level (S_{SM}); cluster-groups E, F, G, I and J*

Values are the number of strains with positive character states.

	Cluster-group E						Cluster-group F										Cluster-group G	Cluster-group I	Cluster-group J			
	Streptomyces pyridomyceticus	'Cluster A/B'	Acidophilic isolates	*Nocardia* spp.	*Streptomyces alboflavus*	*Streptoverticillium netropsis*	*Streptoverticillium hiroshimense*	*Streptoverticillium blastmyceticum*	*Streptoverticillium biverticillatum*	*Streptomyces griseostramineus*	*Streptomyces luridus*	*Streptomyces xanthochromogenes*	*Streptomyces bikiniensis*	*Kitasatoa* spp.	*Streptomyces misakiensis*	*Streptomyces psammoticus*	*Streptomyces fradiae*	*Nocardia* spp.	*Streptomyces viridoflavus*	*Streptomyces clavuligerus*	Acidophilic isolates	*Actinomadura pelletieri*
Cluster number ...	48	49	51	52	54	56	57	58	59	60	62	63	64	65	66	67	68	69	70	71	72	73
Number of strains ...	2	2	2	2	3	4	2	5	3	2	3	3	2	4	3	2	2	2	3	2	5	2
Morphology and pigmentation:																						
1. Presence of spores (aerial mycelium)	0	2	2	2	0	4	2	5	3	2	3	3	2	4	3	2	2	2	0	2	5	0
Spore chain morphology:																						
2. Rectiflexibiles	0	0	2	2	0	0	0	0	0	0	1	3	2	4	2	1	0	2	0	0	4	0
3. Retinaculiaperti	0	1	0	0	0	0	0	0	0	1	0	0	0	0	2	0	2	0	0	1	0	0
4. Spirales	0	1	0	0	0	1	0	0	0	1	2	0	0	0	0	1	1	0	0	1	1	0
5. Verticillati	0	0	0	0	0	3	2	5	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Spore chain ornamentation:																						
6. Smooth	0	2	2	2	0	4	2	5	3	1	3	3	2	4	3	2	2	2	0	2	2	0
7. Warty	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8. Spiny	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
9. Hairy	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0
10. Rugose	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11. Production of aerial spore mass	0	1	1	2	0	4	2	5	3	2	3	3	2	4	3	1	2	2	0	2	5	0
Colour of aerial spore mass:																						
12. Red	0	0	1	0	0	3	2	2	2	0	2	1	0	1	0	1	2	2	0	0	1	0
13. Yellow	0	0	0	1	0	1	0	2	0	0	0	1	0	0	0	0	0	0	0	0	1	0
14. Grey	0	0	0	0	0	0	0	0	0	1	1	0	2	3	2	0	0	0	0	0	1	0
15. Green	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0
16. Blue	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
17. Violet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Cluster number ...	48	49	51	52	54	56	57	58	59	60	62	63	64	65	66	67	68	69	70	71	72	73
Number of strains ...	2	2	2	2	3	4	2	5	3	2	3	3	2	4	3	2	2	2	3	2	5	2
18. White	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	2	0
19. No distinctive substrate mycelial pigments	2	2	1	2	3	4	1	5	3	1	3	3	2	4	3	2	2	1	3	2	5	0
Pigmentation of substrate mycelium:																						
20. Red/orange	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	2
21. Green	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22. Blue	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23. Violet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24. Production of diffusible pigments	0	0	0	0	0	1	2	0	0	1	0	0	0	4	1	1	0	0	0	0	0	0
Pigmentation of diffusible pigments:																						
25. Red/orange	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
26. Yellow/brown	0	0	0	0	0	0	1	0	0	0	0	0	0	4	1	1	0	0	0	0	0	0
27. Green	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28. Blue	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29. Violet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30. Sensitivity of substrate pigment to pH	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
31. Sensitivity of diffusible pigment to pH	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32. Melanin production on peptone/yeast/iron agar	0	0	0	0	2	3	2	2	1	2	2	3	1	3	0	1	0	0	0	0	0	0
33. Melanin production on tyrosine agar	0	0	0	0	1	0	2	0	0	2	1	3	0	0	2	0	0	0	0	0	0	0
34. Fragmentation of mycelium	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
35. Sclerotia formation	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66. Sporulation on substrate mycelium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antimicrobial activity against:																						
54. *Bacillus subtilis* NCIB 3610	0	0	0	0	2	3	2	5	0	1	3	1	2	2	3	0	2	0	0	2	0	1
55. *Pseudomonas fluorescens* NCIB 9046	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
56. *Escherichia coli* NCIB 9132	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2	0	0	1	0	0
57. *Micrococcus luteus* NCIB 196	0	0	2	0	2	4	1	5	1	2	3	3	2	2	3	1	2	0	0	1	0	0
58. *Candida albicans* CBS 562	0	0	0	0	1	4	0	2	1	0	0	0	0	0	1	2	0	0	0	0	0	0
59. *Saccharomyces cerevisiae* CBS 1171	0	0	0	0	0	4	0	1	2	0	0	0	1	0	1	0	1	0	0	0	0	0
60. *Streptomyces murinus* ISP 5091	1	1	0	0	3	4	2	4	1	2	3	2	0	3	1	0	1	0	1	2	0	1
61. *Aspergillus niger* LIV 131	0	0	0	0	2	4	1	4	3	0	0	0	1	2	2	0	1	0	0	1	0	0
Enzyme activity:																						
47. Lecithinase } on egg-yolk medium	0	0	0	0	2	4	2	3	3	2	2	2	2	3	1	0	2	0	0	0	0	0
48. Proteolysis } on egg-yolk medium	0	1	2	0	1	4	2	4	3	1	3	2	2	4	3	2	2	0	2	2	2	0
49. Lipolysis } on egg-yolk medium	0	0	0	1	2	4	2	3	3	1	1	1	2	1	2	1	2	0	3	2	0	0
50. Pectin hydrolysis	0	0	2	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0
51. Chitin hydrolysis	0	0	0	1	0	2	1	0	0	0	1	1	1	2	0	0	1	0	0	0	0	0
52. Nitrate reduction	1	0	0	2	0	1	2	0	2	1	0	2	1	4	0	0	1	1	0	0	0	2

Table 6 (*continued*)

Cluster number ...	48	49	51	52	54	56	57	58	59	60	62	63	64	65	66	67	68	69	70	71	72	73
Number of strains ...	2	2	2	2	3	4	2	5	3	2	3	3	2	4	3	2	2	2	3	2	5	2
53. Hydrogen sulphide production	2	2	1	2	3	3	0	2	0	1	3	3	2	3	3	2	0	2	2	1	1	2
62. Hippurate hydrolysis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63. β-Lactamase production on YPG agar	0	2	0	2	0	1	2	3	3	2	1	3	1	2	3	0	2	0	3	0	0	0
64. β-Lactamase production on Beecham's FS agar	0	2	0	1	0	1	2	4	3	2	1	3	0	2	3	0	2	0	3	0	0	0
65. Production of *Klebsiella* β-lactamase inhibitor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Degradation of:																						
67. Hypoxanthine	1	2	0	2	1	4	2	3	2	2	3	3	2	4	3	2	0	0	2	1	4	2
68. Guanine	2	2	0	2	2	3	2	0	0	2	3	3	1	4	3	0	1	0	2	2	2	0
69. Elastin	1	1	0	1	2	4	2	3	0	2	2	3	2	4	3	2	1	0	2	2	0	2
70. L-Tyrosine	2	0	2	1	3	4	2	5	3	2	2	3	2	4	3	2	0	2	3	2	4	2
71. Adenine	1	2	1	0	3	2	0	0	0	0	2	3	2	4	3	2	2	2	2	2	0	0
72. Xanthine	1	2	0	0	2	3	1	0	0	2	3	3	1	4	2	1	0	0	0	0	0	0
73. DNA	1	0	1	1	1	4	2	3	1	1	3	3	2	4	0	1	1	2	2	2	2	1
74. RNA	2	2	0	2	3	4	2	5	3	2	3	3	2	1	3	1	2	1	3	2	1	0
75. Tween 80	2	2	2	2	3	4	2	5	3	2	2	3	2	4	3	2	2	1	3	2	3	2
76. Starch	2	2	1	0	3	3	2	3	2	0	1	3	2	3	3	2	1	0	2	2	4	0
77. Xylan	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0
78. Casein	1	1	2	1	3	4	2	4	3	2	3	3	2	4	3	2	2	1	3	2	5	2
79. Testosterone	2	1	1	2	0	3	1	4	2	2	2	3	2	3	2	2	0	1	1	2	2	0
80. Urea	1	0	1	2	3	2	1	5	1	2	3	1	2	4	0	2	1	2	0	0	0	0
81. Allantoin	0	0	1	2	3	1	0	0	1	2	3	1	2	4	0	2	0	2	0	0	0	0
82. Gelatin	2	2	2	1	3	4	2	5	3	2	3	3	2	4	3	2	2	0	3	2	3	2
83. Aesculin	2	2	2	2	3	4	1	4	2	2	3	3	2	4	3	0	2	2	2	2	5	0
84. Arbutin	2	1	2	2	1	3	0	0	2	0	3	3	0	3	0	0	2	1	1	1	5	0
Resistance to antibiotics ($\mu g\ ml^{-1}$):																						
85. Gentamicin (100)	0	0	2	1	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0
86. Neomycin (50)	1	1	2	2	3	2	2	4	2	0	0	1	2	3	2	1	1	1	0	0	5	0
87. Streptomycin (100)	0	0	0	2	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	3	1
88. Tobramycin (50)	1	1	2	1	3	0	2	2	1	0	0	0	2	0	2	0	0	0	0	0	3	0
89. Rifampicin (50)	0	0	2	1	3	0	1	0	1	0	1	1	0	4	0	0	0	1	0	0	0	2
90. Cephaloridine (100)	2	2	2	2	3	4	2	5	3	2	3	3	2	4	3	2	2	2	1	2	5	1
91. Vancomycin (50)	0	0	2	2	3	0	1	2	0	0	0	0	0	0	0	2	0	0	0	0	0	1
92. Dimethylchlortetracycline (500)	0	0	0	0	1	0	1	3	1	0	0	0	0	0	1	2	0	0	0	0	0	0
93. Oleandomycin (100)	0	1	2	2	3	0	1	2	0	1	1	0	1	3	0	0	0	2	0	0	0	2
94. Lincomycin (100)	2	2	2	2	3	4	2	5	1	2	3	2	2	4	2	0	2	2	1	2	5	2
95. Penicillin G (10 i.u.)	1	2	2	2	3	4	2	4	3	0	2	1	2	1	0	0	1	0	1	2	0	0

Cluster number ...	48	49	51	52	54	56	57	58	59	60	62	63	64	65	66	67	68	69	70	71	72	73
Number of strains ...	2	2	2	2	3	4	2	5	3	2	3	3	2	4	3	2	2	2	3	2	5	2
Growth at:																						
96. 4 °C	0	0	0	0	0	3	1	0	0	0	0	2	0	0	0	0	0	1	0	0	4	0
97. 10 °C	1	1	1	1	3	4	2	4	2	2	2	3	1	1	3	1	1	2	0	1	5	0
98. 37 °C	1	1	0	2	2	2	2	5	3	2	3	0	1	4	1	2	2	0	2	0	0	2
99. 45 °C	1	1	0	0	0	0	0	5	2	1	1	0	1	0	1	0	2	0	0	0	0	2
100. pH 4·3	0	0	2	0	0	0	0	2	0	0	0	0	1	0	1	1	0	0	0	0	4	0
Growth in the presence of (%, *w/v*):																						
101. Sodium chloride (4)	2	2	0	2	3	4	2	3	3	2	3	0	0	4	1	0	2	2	1	0	0	0
102. Sodium chloride (7)	2	2	0	0	0	2	1	1	2	2	0	0	0	1	0	0	0	0	1	0	0	0
103. Sodium chloride (10)	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
104. Sodium chloride (13)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
105. Sodium azide (0·01)	0	1	0	0	1	1	1	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0
106. Sodium azide (0·02)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107. Phenylethanol (0·1)	1	2	0	2	3	4	2	4	3	2	2	2	1	3	3	2	2	2	0	1	0	2
108. Phenylethanol (0·3)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
109. Phenol (0·1)	1	2	0	1	3	3	2	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0
110. Potassium tellurite (0·001)	1	2	0	1	1	3	1	1	3	1	0	0	0	0	2	2	2	2	2	0	0	2
111. Potassium tellurite (0·01)	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
112. Thallous acetate (0·001)	0	0	2	1	1	0	0	0	3	0	0	0	1	0	0	0	0	2	0	0	4	0
113. Thallous acetate (0·01)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
114. Crystal violet (0·0001)	0	2	2	1	3	4	2	4	3	2	1	1	2	3	3	2	1	2	0	0	2	2
Growth on sole nitrogen source (*0·1*%, *w/v*):																						
36. DL-α-Amino-n-butyric acid	0	0	0	2	0	2	0	1	0	2	1	1	1	0	1	0	0	2	0	0	0	0
37. Potassium nitrate	0	0	0	2	2	4	2	5	0	2	3	3	1	4	3	0	2	2	2	0	0	1
38. L-Cysteine	0	0	0	0	0	3	0	3	2	1	2	0	1	0	1	0	0	2	0	0	0	0
39. L-Valine	1	0	0	1	0	2	2	2	3	0	1	0	1	0	2	1	0	2	1	0	4	0
40. L-Threonine	0	0	0	1	0	4	2	4	0	1	3	3	2	1	3	2	2	1	2	1	5	1
41. L-Serine	0	1	0	2	0	4	2	5	3	1	3	3	1	1	3	1	2	2	2	1	4	0
42. L-Phenylalanine	0	0	0	1	3	1	2	3	3	2	3	2	1	0	1	0	1	0	1	0	5	0
43. L-Methionine	0	0	0	1	0	2	0	0	1	0	0	1	0	0	0	1	0	1	1	0	0	0
44. L-Histidine	0	0	0	2	0	0	1	2	3	1	2	2	2	0	3	1	0	2	2	0	5	1
45. L-Arginine	0	0	0	2	1	4	2	5	3	2	3	3	2	4	3	2	1	2	3	2	5	0
46. L-Hydroxyproline	0	0	0	0	2	2	0	0	0	0	2	1	0	0	3	1	0	0	1	0	5	0

Table 6 (*continued*)

Cluster number ...	48	49	51	52	54	56	57	58	59	60	62	63	64	65	66	67	68	69	70	71	72	73
Number of strains ...	2	2	2	2	3	4	2	5	3	2	3	3	2	4	3	2	2	2	3	2	5	2
Growth on sole carbon source (1·0%, w/v):																						
115. L-Arabinose	2	2	2	2	3	0	0	0	0	1	3	2	0	4	2	0	1	1	0	1	1	0
116. Sucrose	2	1	2	2	1	1	1	1	1	2	1	1	1	1	2	1	0	2	0	0	0	0
117. D-Xylose	2	1	0	2	3	0	0	0	0	2	3	1	0	0	2	0	2	1	0	1	0	0
118. *meso*-Inositol	1	2	2	1	2	4	2	2	2	0	1	0	0	3	0	0	0	1	1	1	0	0
119. Mannitol	2	2	2	2	3	2	0	1	1	0	0	1	0	1	0	0	0	2	1	1	0	0
120. D-Fructose	2	2	2	2	3	4	2	3	2	2	3	1	2	3	3	2	0	2	3	0	0	0
121. L-Rhamnose	1	2	2	1	1	2	0	0	2	0	0	0	0	0	0	0	2	2	1	1	0	0
122. Raffinose	2	0	2	2	2	2	0	1	0	2	0	1	0	0	2	0	1	2	1	0	1	1
123. D-Melezitose	2	2	2	1	1	2	0	2	1	0	1	1	0	4	1	0	1	1	0	0	0	0
124. D-Mannose	2	2	2	2	3	4	2	3	3	2	3	3	2	4	2	2	1	2	1	1	1	0
125. D-Lactose	2	0	2	2	2	0	1	1	0	1	0	2	1	0	1	0	1	1	0	0	0	1
126. Inulin	1	0	2	2	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0
127. Adonitol	1	2	0	2	2	0	0	0	1	0	3	0	0	0	0	0	0	1	1	1	0	0
128. Salicin	2	0	1	2	2	3	0	0	1	0	3	3	1	3	0	0	1	1	1	1	0	0
129. Trehalose	2	2	2	2	3	4	2	5	3	2	3	3	2	3	3	2	2	2	1	2	0	2
130. D-Melibiose	2	2	2	2	1	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0
131. Dextran	2	1	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132. D-Galactose	2	2	1	2	3	2	0	4	1	2	1	1	2	2	3	1	0	1	3	1	0	1
133. Cellobiose	2	0	2	2	3	2	0	1	0	2	3	3	1	2	3	0	0	2	1	1	0	0
134. Xylitol	1	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1
135. Sodium acetate (0·1%, w/v)	2	2	0	2	3	4	2	2	2	2	1	0	2	2	2	1	0	1	1	1	0	1
136. Sodium citrate (0·1%, w/v)	1	2	1	1	2	2	1	2	2	1	3	1	2	4	2	2	2	1	1	1	1	1
137. Sodium malonate (0·1%, w/v)	1	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
138. Sodium propionate (0·1%, w/v)	1	2	0	2	2	2	1	0	0	0	1	0	1	3	3	2	2	1	1	0	0	2
139. Sodium pyruvate (0·1%, w/v)	1	1	2	2	0	3	1	1	3	0	2	1	1	2	2	0	1	1	1	0	0	0

as possible the designations of the cluster-groups and clusters defined by the S_{SM} coefficient have been preserved.

Composition of cluster-groups. The composition of four of the major cluster-groups recognized in the S_{SM}/UPGMA analysis was altered in the corresponding S_J run, while major cluster-groups B and C and the minor cluster-group D were not recovered at all. Cluster-group A contained 343 strains, which included the seven *S. rimosus* strains of cluster 42, the remaining strain of cluster-group B, *S. amakusaensis* ISP 5219, forming a single member cluster-group (Table 8). *Streptomyces badius* ISP 5139, *S. ramulosus* ISP 5100 and organisms previously classified in cluster 43 (*S. griseoluteus*) and 44 (*S. pactum*) were also recovered in cluster-group A. The remaining three phena in cluster-group C, clusters 45 (*S. aurantiacus*), 46 (*S. varsoviensis*) and 47 (*S. tubercidicus*), were each raised to the status of cluster-groups. *Streptomyces sulphureus* ISP 5104, the final strain in cluster-group C, formed a single member cluster, which was closely related to the strains in cluster 46. Cluster-group A also gained strains from cluster-groups E and F. Thus, the fodder isolates forming cluster 49 of cluster-group E were each recovered as single member clusters on the periphery of cluster-group A. The latter also encompassed all the cluster 62 (*S. luridus*) strains of cluster-group F. *Microellobosporia violacea* M297 and *S. massasporeus* ISP 5035, which formed cluster-group D in the S_{SM} analysis, were also classified in cluster-group A (cluster 19C) and as a single member cluster-group, respectively.

Minor cluster-groups G and H were recovered in their entirety. Cluster-group I was again recognized, though one of its three strains, *S. finlayi* ISP 5218, formed one of the 21 single member cluster-groups defined in addition to '*Nocardia*' *capreola* ISP 5225. Cluster-group E was restricted to strains previously classified in clusters 52 (*Nocardia* spp.), 53 ('*N.*' *mediterranea*) and 54 (*S. alboflavus*), with *A. helvata* A5 forming a single member cluster-group and the strains in clusters 48 (*S. pyridomyceticus*), 50 (*Actinomadura* spp.) and 51 (acidophilic isolates) comprising discrete cluster-groups (Table 8).

The remaining taxa of cluster-group F were assigned to three distinct cluster-groups designated F1, F2 and F3 (Table 8). Cluster-group F1 contained most of the strains previously classified in clusters 55 (*Stv. griseocarneum*), 56 (*Stv. netropsis*), 57 (*Stv. hiroshimense*) 58 (*Stv. blastmyceticum*) and 59 (*Stv. biverticillatum*); F2, those from clusters 61 (*S. lavendulae*), 63 (*S. xanthochromogenes*), 64 (*S. bikiniensis*) and 66 (*S. misakiensis*). Cluster-group F3 contained the *Kitasatoa* strains of cluster 65 and *S. xantholiticus* ISP 5244 from cluster 24 (*S. flaveolus*) of cluster-group A. The cluster-group J strains showed little similarity to one another in the S_J/UPGMA analysis. Thus, *Intrasporangium calvum* IC, '*S. luteofluorescens*' ISP 5398, *S. novaecaesareae* ISP 5358 and the organisms in phena 70 (*S. viridoflavus*) and 71 (*S. clavuligerus*) all formed single member cluster-groups. The strains in cluster 72 (acidophilic isolates) were recovered in two cluster-groups, those in 73 (*Actinomadura pelletieri*) also forming a distinct cluster-group (Table 8).

Composition of clusters. All of the major and most of the minor clusters were recognized in the S_J/UPGMA analysis, though in some cases cluster composition was altered (Table 8) and in most instances the phena were arranged differently (cf. Figs 2 and 3). Fifteen of the 22 major clusters were, however, recovered intact, or their composition only marginally altered by the S_J analysis. Thus, clusters 10 (*S. fulvissimus*), 16 (*S. albus*), 17 (*S. griseoviridis*), 32 (*S. violaceoniger*), 42 (*S. rimosus*), and 53 ('*N.*' *mediterranea*) were recovered as before. The strain content of clusters 1 (*S. albidoflavus*), 3 (*S. atroolivaceus*), 6 (*S. violaceus*), 12 (*S. rochei*), 18 (*S. cyaneus*), 21 (*S. griseoruber*), 37 (*S. griseoflavus*) and 40 (*S. phaeochromogenes*) showed some changes (Table 8). Cluster 50 (*Actinomadura* spp.) was also recovered intact, but at the 45% *S*-level. The composition of subcluster 1C was also unaltered, but the two remaining subclusters of cluster 1 (*S. albidoflavus*) showed some changes, notably the inclusion of all three strains of cluster 2 ('*Stv.*' *olivoverticillatum*) in subcluster 1A.

The seven remaining major clusters split into two or more subclusters (Fig. 3). Clusters 5 (*S. exfoliatus*), 20 (*S. olivaceoviridis*) and 29 (*S. lydicus*) were each recovered as two subclusters which were well separated in the case of *S. olivaceoviridis*. Thus, the three *Elytrosporangium* strains of subcluster 20A were found to be quite distinct from the five streptomycetes comprising

Table 7. *Distribution of positive characters to single member clusters defined at the 77·5% similarity level (S_{SM})*

	Actinomadura helvata	*Intrasporangium calvum*	*Microellobosporia violacea*	*'Nocardia capreola'*	*Nocardioides albus*	*Streptomyces albocyaneus*	*Streptomyces amakusaensis*	*Streptomyces aurantiogriseus*	*Streptomyces badius*	*Streptomyces bambergiensis*
Strain no. ...	A5	IC	M297	5225	7801	5197	5219	5138	5139	5590
Cluster-group ...	E	J	D	—	A	A	B	A	C	A
Highest affinity (cluster/strain) with ...	50	ISP 5398	ISP 5035	—	40/41	37	43	18	46/47	37
Morphology and pigmentation:										
1. Presence of spores (aerial mycelium)	1	0	1	1	0	1	1	1	1	1
Spore chain morphology:										
2. Rectiflexibiles	0	0	1	0	0	0	0	0	1	0
3. Retinaculiaperti	0	0	0	0	0	1	0	1	0	1
4. Spirales	1	0	0	1	0	0	1	0	0	0
5. Verticillati	0	0	0	0	0	0	0	0	0	0
Spore chain ornamentation:										
6. Smooth	1	0	1	1	0	0	1	1	1	0
7. Warty	0	0	0	0	0	1	0	0	0	0
8. Spiny	0	0	0	0	0	0	0	0	0	0
9. Hairy	0	0	0	0	0	0	0	0	0	1
10. Rugose	0	0	0	0	0	0	0	0	0	0
11. Production of aerial spore mass	1	0	0	1	0	1	1	1	1	1
Colour of aerial spore mass:										
12. Red	0	0	0	1	0	0	0	0	0	0
13. Yellow	0	0	0	0	0	1	0	0	1	0
14. Grey	0	0	0	0	0	0	0	1	0	0
15. Green	0	0	0	0	0	0	0	0	0	1
16. Blue	0	0	0	0	0	0	1	0	0	0
17. Violet	0	0	0	0	0	0	0	0	0	0
18. White	1	0	0	0	0	0	0	0	0	0
19. No distinctive substrate mycelial pigments	1	1	0	1	1	0	1	1	1	0
Pigmentation of substrate mycelium:										
20. Red/orange	0	0	0	0	0	0	0	0	0	1
21. Green	0	0	0	0	0	0	0	0	0	0
22. Blue	0	0	0	0	0	1	0	0	0	0
23. Violet	0	0	1	0	0	0	0	0	0	0
24. Production of diffusible pigments	0	0	1	1	0	0	0	1	1	1
Pigmentation of diffusible pigments:										
25. Red/orange	0	0	0	0	0	0	0	0	0	1
26. Yellow/brown	0	0	0	1	0	0	0	1	1	0
27. Green	0	0	0	0	0	0	0	0	0	0
28. Blue	0	0	0	0	0	0	0	0	0	0
29. Violet	0	0	1	0	0	0	0	0	0	0
30. Sensitivity of substrate pigment to pH	0	0	1	0	0	1	1	0	0	1
31. Sensitivity of diffusible pigment to pH	0	0	1	0	0	0	0	0	0	1
32. Melanin production on peptone/yeast/iron agar	0	0	0	0	0	0	0	1	0	0
33. Melanin production on tyrosine agar	0	0	0	0	0	0	0	1	1	0
34. Fragmentation of mycelium	0	1	0	0	1	0	0	0	0	0
35. Sclerotia formation	0	0	0	1	0	0	0	0	0	0
66. Sporulation on substrate mycelium	0	0	1	0	0	0	0	0	0	0

Table 7 (*continued*)

Character	*Streptomyces cyaneogriseus* 5534 H ISP 5167	*Streptomyces finlayi* 5218 I 69	*Streptomyces fragilis* 5044 G 68	*Streptomyces gelaticus* 5065 A 7/8	*Streptomyces lateritius* 5163 H ISP 5534	*Streptomyces luteofluorescens* 5398 J IC	*Streptomyces massasporeus* 5035 D M297	*Streptomyces mediocidicus* 5021 F 55–59	*Streptomyces moderatus* 5529 A 10	*Streptomyces novaecaesarae* 5358 J 73	*Streptomyces ramulosus* 5100 C 43	*Streptomyces sulphureus* 5104 C 46	*Streptomyces versipellis* 5491 A 7801	*Streptoverticillium albireticuli* 5051 F 60	*Streptoverticillium baldacci* M363 F 58	*Streptoverticillium kentuckense* 5052 F 55–57	*Streptoverticillium ladakanum* 5587 F 64	*Streptoverticillium thioluteum* 5027 F 55–59
1.	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	0
2.	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
3.	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
4.	1	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0
5.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
6.	1	0	1	1	1	0	1	0	1	0	1	1	1	1	1	1	1	0
7.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
8.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11.	1	1	1	0	1	0	1	0	1	0	1	0	1	1	1	1	1	0
12.	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0
13.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14.	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
15.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
18.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
19.	1	0	1	0	0	1	0	1	0	0	1	1	1	1	0	1	1	1
20.	0	0	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0	0
21.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
24.	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0
25.	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0
26.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
27.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
28.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
30.	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0
31.	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0
32.	1	0	0	0	1	0	1	1	1	0	0	0	1	1	1	0	0	0
33.	1	0	0	0	1	0	1	0	0	0	0	0	1	1	0	1	0	0
34.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

Table 7 (*continued*)

Strain no. ...	A5	IC	M297	5225	7801	5197	5219	5138	5139	5590
Cluster-group ...	E	J	D	—	A	A	B	A	C	A
Highest affinity (cluster/strain) with ...	50	ISP 5398	ISP 5035	—	40/41	37	43	18	46/47	37
Antimicrobial activity against:										
54. *Bacillus subtilis* NCIB 3610	0	0	0	0	0	0	1	0	0	0
55. *Pseudomonas fluorescens* NCIB 9046	0	0	0	0	0	0	1	0	0	0
56. *Escherichia coli* NCIB 9132	0	0	0	0	0	0	0	0	0	0
57. *Micrococcus luteus* NCIB 196	0	0	0	0	0	0	1	0	1	0
58. *Candida albicans* CBS 562	0	0	0	0	0	0	1	0	0	0
59. *Saccharomyces cerevisiae* CBS 1171	0	0	0	0	0	0	0	0	0	0
60. *Streptomyces murinus* ISP 5091	0	0	0	0	0	0	1	0	1	1
61. *Aspergillus niger* LIV 131	0	0	0	0	0	0	1	0	0	0
Enzyme activity:										
47. Lecithinase } on egg-yolk medium	0	0	0	0	0	0	0	0	0	0
48. Proteolysis } on egg-yolk medium	1	0	0	0	1	0	0	1	1	1
49. Lipolysis } on egg-yolk medium	1	0	0	0	1	1	0	0	1	1
50. Pectin hydrolysis	0	0	0	0	0	0	0	0	1	1
51. Chitin hydrolysis	0	0	0	1	0	0	0	0	1	1
52. Nitrate reduction	1	1	1	0	1	1	0	1	0	1
53. Hydrogen sulphide production	0	0	1	0	1	1	1	0	1	0
62. Hippurate hydrolysis	0	0	0	0	1	1	0	1	1	0
63. β-Lactamase production on YPG agar	0	0	1	1	1	0	1	1	0	0
64. β-Lactamase production on Beecham's FS agar	1	0	1	1	1	0	1	1	0	0
65. Production of *Klebsiella* β-lactamase inhibitor	0	0	0	0	0	0	0	0	0	0
Degradation of:										
67. Hypoxanthine	0	0	1	1	1	1	0	1	1	1
68. Guanine	0	0	0	1	1	0	1	1	1	0
69. Elastin	1	1	0	1	1	0	1	0	1	1
70. L-Tyrosine	0	0	1	1	1	1	1	1	1	0
71. Adenine	0	0	1	0	0	1	1	1	1	1
72. Xanthine	0	0	0	1	1	0	0	0	1	0
73. DNA	1	1	1	1	1	1	1	1	1	1
74. RNA	1	0	1	1	1	1	1	1	1	1
75. Tween 80	0	1	0	1	1	0	1	1	1	1
76. Starch	0	0	1	1	1	1	0	1	0	1
77. Xylan	0	0	0	1	0	0	0	1	1	0
78. Casein	1	1	1	1	1	1	1	1	1	1
79. Testosterone	1	0	1	1	1	1	0	1	1	1
80. Urea	0	0	0	1	0	0	1	1	1	1
81. Allantoin	0	0	0	0	0	0	0	0	1	1
82. Gelatin	1	1	1	1	1	1	1	1	1	1
83. Aesculin	1	1	1	1	1	1	1	1	1	1
84. Arbutin	1	1	1	0	0	1	0	0	1	1
Resistance to antibiotics ($\mu g\ ml^{-1}$):										
85. Gentamicin (100)	1	1	0	1	0	0	0	0	0	0
86. Neomycin (50)	1	1	0	1	0	0	0	0	0	0
87. Streptomycin (100)	0	0	0	0	0	0	0	0	0	0
88. Tobramycin (50)	0	1	0	1	0	0	0	0	0	0
89. Rifampicin (50)	1	0	1	1	0	0	0	0	1	0
90. Cephaloridine (100)	1	1	1	1	1	1	0	1	1	1
91. Vancomycin (50)	0	0	0	0	0	0	0	0	0	0
92. Dimethylchlortetracycline (500)	0	0	0	0	0	0	0	0	0	0
93. Oleandomycin (100)	1	0	1	0	1	1	0	1	0	1
94. Lincomycin (100)	1	0	1	1	1	1	1	1	1	0
95. Penicillin G (10 i.u.)	0	0	1	0	0	0	0	0	1	0
Growth at:										
96. 4 °C	0	0	0	0	1	1	0	0	1	0
97. 10 °C	0	1	1	0	1	1	1	0	1	1
98. 37 °C	1	1	1	1	1	0	0	1	1	1
99. 45 °C	1	0	0	1	0	0	0	1	0	0
100. pH 4·3	0	0	0	0	0	0	0	0	0	0

Table 7 (*continued*)

Character	5534 H ISP 5167	5218 I 69	5044 G 68	5065 A 7/8	5163 H ISP 5534	5398 J IC	5035 D M297	5021 F 55–59	5529 A 10	5358 J 73	5100 C 43	5104 C 46	5491 A 7801	5051 F 60	M363 F 58	5052 F 55–57	5587 F 64	5027 F 55–59
54.	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0	1
55.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57.	1	0	1	0	1	0	0	1	0	1	1	0	0	1	1	1	1	1
58.	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1
59.	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0
60.	1	0	1	0	1	0	1	1	0	0	1	0	0	0	1	1	0	1
61.	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	1	1
47.	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1
48.	0	1	1	1	1	0	0	1	1	1	1	1	0	1	1	1	1	1
49.	0	1	1	1	1	0	0	0	1	0	1	1	1	1	1	0	1	0
50.	0	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0
51.	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52.	1	1	0	1	1	1	1	0	1	1	0	1	1	1	0	1	0	0
53.	1	1	1	1	0	0	0	1	0	1	1	1	0	0	0	1	1	0
62.	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1
63.	0	0	1	1	0	0	1	0	1	0	1	0	1	1	1	1	0	0
64.	0	0	1	1	0	0	1	0	1	0	1	0	1	0	1	0	0	0
65.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
67.	1	0	1	0	1	0	1	1	1	0	1	1	1	1	0	1	1	0
68.	1	0	1	1	1	1	0	0	1	1	1	0	1	0	0	1	0	0
69.	0	0	1	1	1	0	0	1	1	0	1	1	0	1	0	0	1	1
70.	1	0	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0
71.	1	1	1	1	1	0	1	0	1	1	1	1	1	0	0	1	0	0
72.	1	0	0	1	1	0	1	0	1	0	1	1	0	1	0	0	1	0
73.	0	1	1	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1
74.	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
75.	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1
76.	1	1	1	0	1	0	0	1	1	1	1	1	0	1	0	0	0	0
77.	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
78.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
79.	0	0	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	0
80.	0	1	0	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1
81.	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	1	0
82.	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
83.	1	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1	1	1
84.	1	0	1	1	1	1	1	0	0	1	0	0	1	0	0	1	1	0
85.	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0
86.	0	0	0	0	1	1	0	1	1	0	1	0	0	0	1	1	1	0
87.	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1
88.	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0
89.	1	1	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	1
90.	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1	1	1	0
91.	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0
92.	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1
93.	1	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1
94.	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
95.	0	0	0	1	1	1	0	1	1	0	1	1	0	1	1	1	1	1
96.	0	1	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0
97.	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	0	0
98.	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
99.	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	1	0	1
100.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 7 (*continued*)

Strain no. ...	A5	IC	M297	5225	7801	5197	5219	5138	5139	5590
Cluster-group ...	E	J	D	—	A	A	B	A	C	A
Highest affinity (cluster/strain) with ...	50	ISP 5398	ISP 5035	—	40/41	37	43	18	46/47	37
Growth in the presence of (%, *w/v*):										
101. Sodium chloride (4)	0	0	1	0	1	1	1	1	1	1
102. Sodium chloride (7)	0	0	0	0	0	0	0	0	1	0
103. Sodium chloride (10)	0	0	0	0	0	0	0	0	1	0
104. Sodium chloride (13)	0	0	0	0	0	0	0	0	0	0
105. Sodium azide (0·01)	0	0	0	0	1	0	0	0	1	0
106. Sodium azide (0·02)	0	0	0	0	1	0	0	0	1	0
107. Phenylethanol (0·1)	1	1	1	1	1	1	1	1	1	1
108. Phenylethanol (0·3)	0	0	0	0	1	0	0	0	0	0
109. Phenol (0·1)	0	0	1	0	1	1	0	0	1	1
110. Potassium tellurite (0·001)	1	1	1	1	1	1	1	1	1	1
111. Potassium tellurite (0·01)	1	1	0	1	1	0	0	0	0	0
112. Thallous acetate (0·001)	0	1	1	0	0	1	1	0	0	1
113. Thallous acetate (0·01)	0	0	0	0	0	0	0	0	0	0
114. Crystal violet (0·0001)	1	0	1	0	1	0	1	0	1	0
Growth on sole nitrogen source (*0·1*%, *w/v*):										
36. DL-α-Amino-n-butyric acid	0	0	0	1	1	0	0	0	0	0
37. Potassium nitrate	0	1	1	1	1	1	0	0	1	1
38. L-Cysteine	0	1	0	0	0	0	0	0	0	0
39. L-Valine	0	0	1	1	1	1	0	0	0	0
40. L-Threonine	0	0	1	1	1	1	1	1	0	1
41. L-Serine	0	1	1	1	1	1	1	1	1	1
42. L-Phenylalanine	0	1	0	1	0	0	1	0	0	0
43. L-Methionine	0	1	0	1	1	0	0	1	0	0
44. L-Histidine	0	0	1	1	1	1	0	1	1	1
45. L-Arginine	1	1	1	1	0	1	0	1	1	1
46. L-Hydroxyproline	0	0	0	1	0	0	0	0	0	0
Growth on sole carbon source (*1·0*%, *w/v*):										
115. L-Arabinose	1	0	1	1	1	1	1	1	1	0
116. Sucrose	1	0	1	0	0	0	0	1	1	0
117. D-Xylose	1	1	1	0	1	1	1	1	1	0
118. *meso*-Inositol	1	0	1	1	0	1	1	1	0	1
119. Mannitol	0	1	1	1	1	1	1	1	1	1
120. D-Fructose	1	1	1	0	1	1	1	1	1	1
121. L-Rhamnose	0	1	1	0	1	1	0	1	0	1
122. Raffinose	0	0	1	1	0	0	1	1	0	0
123. D-Melezitose	0	0	1	0	0	1	0	1	0	0
124. D-Mannose	1	0	1	1	1	1	1	1	0	1
125. D-Lactose	0	0	1	0	1	1	1	1	0	0
126. Inulin	0	0	1	0	0	0	1	1	0	0
127. Adonitol	1	0	1	0	1	0	1	1	0	0
128. Salicin	1	1	1	0	0	0	1	1	0	1
129. Trehalose	1	1	0	0	1	1	1	1	0	1
130. D-Melibiose	1	0	1	1	0	0	1	1	0	1
131. Dextran	0	0	0	1	0	0	0	0	0	1
132. D-Galactose	0	0	0	1	1	0	1	1	0	0
133. Cellobiose	1	1	1	1	1	1	1	1	0	1
134. Xylitol	0	0	0	0	1	0	1	1	0	0
135. Sodium acetate (0·1%, w/v)	0	0	1	0	0	1	1	1	0	0
136. Sodium citrate (0·1%, w/v)	0	0	0	0	0	1	1	1	0	1
137. Sodium malonate (0·1%, w/v)	0	0	0	0	0	1	0	1	0	0
138. Sodium propionate (0·1%, w/v)	0	0	0	0	1	1	1	1	0	1
139. Sodium pyruvate (0·1%, w/v)	1	1	0	1	0	1	1	1	0	1

Table 7 (*continued*)

Character	5534 H ISP 5167	5218 I 69	5044 G 68	5065 A 7/8	5163 H ISP 5534	5398 J IC	5035 D M297	5021 F 55–59	5529 A 10	5358 J 73	5100 C 43	5104 C 46	5491 A 7801	5051 F 60	M363 F 58	5052 F 55–57	5587 F 64	5027 F 55–59
101.	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
102.	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0
103.	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
104.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
105.	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0	1
106.	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0
107.	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1
108.	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
109.	1	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0	0	0
110.	0	1	1	1	0	0	0	1	0	1	0	1	1	1	0	0	0	0
111.	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
112.	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0
113.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
114.	1	1	1	0	1	0	0	1	1	1	0	1	1	1	1	0	0	0
36.	0	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0	1	0
37.	1	1	1	0	1	1	1	0	1	1	1	0	1	0	1	1	1	1
38.	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0
39.	0	0	0	1	0	0	0	1	1	1	1	1	0	0	1	0	1	1
40.	1	1	0	1	1	0	1	0	1	0	0	0	0	0	1	1	1	1
41.	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1
42.	0	1	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0
43.	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44.	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	1
45.	1	1	0	1	1	0	1	1	1	1	1	0	0	1	1	1	1	1
46.	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0
115.	1	1	1	0	1	0	1	0	1	0	0	1	1	0	0	0	0	0
116.	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0
117.	1	1	1	1	1	1	1	0	1	1	0	0	1	0	0	0	0	0
118.	0	0	0	1	0	0	1	1	1	0	0	0	1	1	1	1	1	1
119.	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	0	0	0
120.	1	0	0	0	1	0	1	1	1	1	1	0	1	1	0	1	1	0
121.	1	0	0	1	1	1	1	0	1	0	1	0	0	1	0	0	0	0
122.	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	1	0	0
123.	0	0	0	1	0	0	1	0	0	1	0	1	0	1	1	0	1	0
124.	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
125.	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0
126.	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
127.	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	1	0	0
128.	1	0	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	1
129.	1	0	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1
130.	0	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	0	0
131.	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0
132.	0	1	1	1	0	1	1	1	1	0	1	0	1	1	1	1	1	0
133.	1	1	1	1	0	1	0	1	1	1	0	0	1	1	1	1	0	0
134.	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0
135.	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0
136.	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	1	0	0
137.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138.	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0
139.	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1

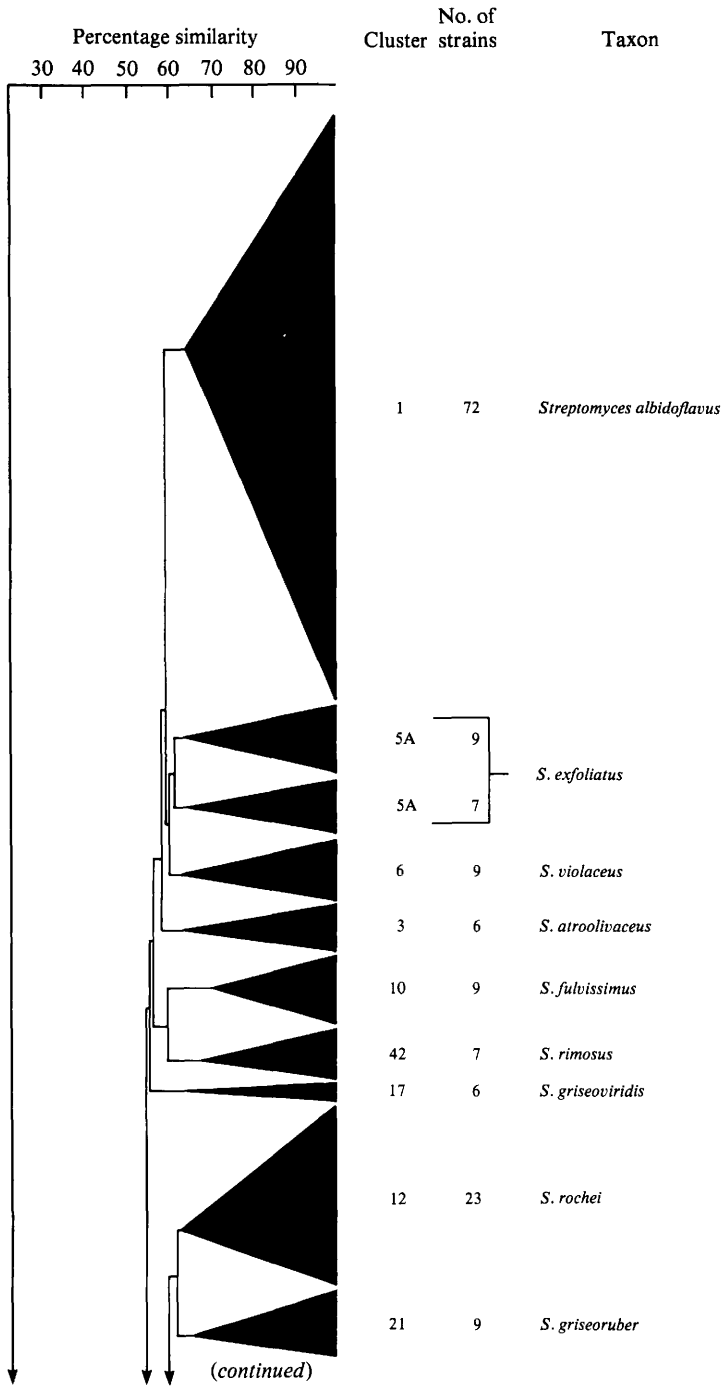


Fig. 3. A simplified dendrogram showing the relationships between some of the major and minor clusters defined at the 63% similarity level in the S_J/UPGMA analysis.

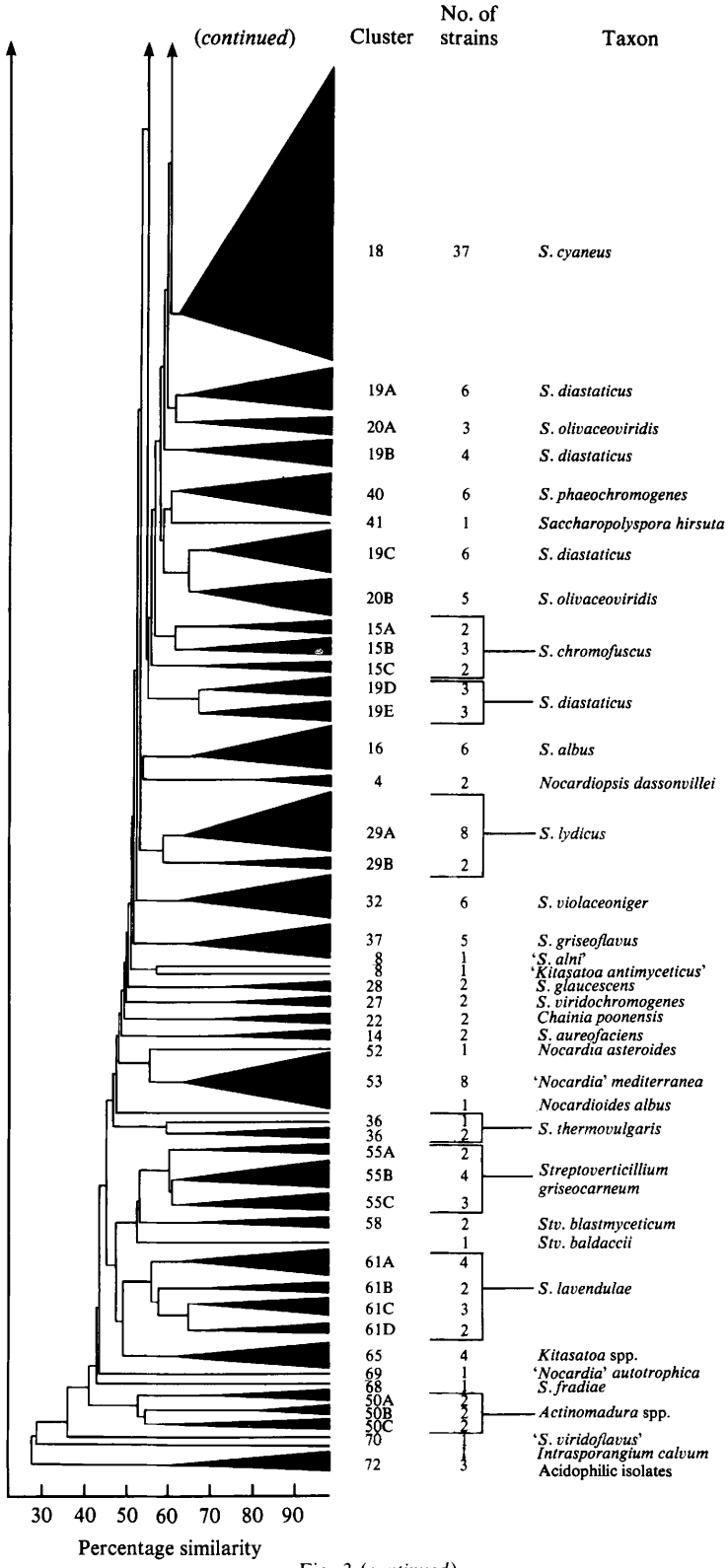


Fig. 3 (*continued*)

Table 8. *Strains assigned to clusters or subclusters (defined at 63%) and cluster-groups (defined at 50%) in the S_J analysis which differ from those defined in the S_{SM}/UPGMA analysis*

S_J assignment				S_{SM} assignment	
Cluster no.	Designation of cluster	Strain no.	Strain name	Cluster no.*	Name of cluster
CLUSTER-GROUP A					
1A	*S. albidoflavus*	5033	*S. aburaviensis*	2	'*Stv*'. *olivoverticillatum*
		5123	*S. herbaricolor*		
		5250	'*Stv.*' *olivoverticillatum*		
		G3	*S. griseus*	15	*S. chromofuscus*
1B	*S. albidoflavus*	5541	'*S. flavochromogenes*'	5	*S. exfoliatus*
		5172	*S. roseofulvus*	14	*S. aureofaciens*
		5230	*S. venezuelae*	6	*S. violaceus*
5A	*S. exfoliatus*	5012	*S. cinereoruber*	5	*S. exfoliatus*
		5064	*S. gardneri*		
		5164	*S. litmocidini*		
		5016	*S. narbonensis*		
		5314	*S. nashvillensis*		
		5278	*S. umbrinus*		
		5279	*S. violaceorectus*		
		5196	*S. zaomyceticus*		
		T1	*Streptomyces* sp.		
5B	*S. exfoliatus*	5060	*S. exfoliatus*		
		5502	*S. filamentosus*		
		5586	*S. hydrogenans*		
		5552	*S. omiyaensis*		
		5174	*S. roseolus*		
		5122	*S. roseosporus*		
		5329	*S. termitum*		
6	*S. violaceus*	5147	*S. cremeus*	1B	*S. albidoflavus*
12	*S. rochei*	5014	*S. eurythermus*	23	*S. microflavus*
		5154	*S. fumanus*	18	*S. cyaneus*
15A	*S. chromofuscus*	5226	*S. argenteolus*	15	*S. chromofuscus*
		5294	'*S. carnosus*'		
15B	*S. chromofuscus*	5270	*Chainia flava*		
		5301	*C. minutisclerotia*		
		5243	*S. viridosporus*		
15C	*S. chromofuscus*	5273	*S. chromofuscus*		
		5089	*S. galbus*		
18	*S. cyaneus*	5256	'*S. coralus*'	19	*S. diastaticus*
		5285	*S. phaeoviridis*		
19A	*S. diastaticus*	M315	*Microellobosporia flavea*		
		5138	*S. aurantiogriseus*	SMC	Cluster-group A
		5263	*S. humidus*	19	*S. diastaticus*
		5031	'*S. minoensis*'		
		5490	'*S. nigellus*'		
		5309	*S. vastus*		*S. diastaticus*
19B	*S. diastaticus*	M301	*M. cinerea*		*S. diastaticus*
		M297	*M. violacea*	SMC	Cluster-group D
		5355	*S. lincolnensis*	19	*S. diastaticus*
		F50	*Streptomyces* sp.	11	*S. prunicolor*
19C	*S. diastaticus*	5496	*S. diastaticus*	19	*S. diastaticus*
		5429	*S. glomeraurantiacus*		
		5451	*S. olivochromogenes*		
		5073	*S. phaeochromogenes*	40	*S. phaeochromogenes*
		5079	'*S. verne*'		
		F1	*Streptomyces* sp.	19	*S. diastaticus*
19D	*S. diastaticus*	5481	*S. galilaeus*	19	*S. diastaticus*
		5560	'*S. tauricus*'		
		5209	*S. violatus*	18	*S. cyaneus*

Table 8 (*continued*)

S_J assignment				S_{SM} assignment	
Cluster no.	Designation of cluster	Strain no.	Strain name	Cluster no.*	Name of cluster
19E	*S. diastaticus*	5262	*S. bottropensis*	19	*S. diastaticus*
		5449	*S. diastatochromogenes*		
		5489	*S. rishiriensis*		
20A	*S. olivaceoviridis*	M086	*Elytrosporangium brasiliense*	20	*S. olivaceoviridis*
		M619	*E. carpinense*		
		M09A	*E. spirale*		
20B	*S. olivaceoviridis*	5528	*S. carnarius*		
		5340	*S. corchorusii*		
		5334	*S. olivaceoviridis*		
		5551	*S. regensis*		
		5220	*S. chibaensis*	24	*S. flaveolus*
21	*S. griseoruber*	5124	*S. indigoferus*	12	*S. rochei*
		5433	'*S. lazureus*'		
29A	*S. lydicus*	5054	'*S. fasiculatus*'	29	*S. lydicus*
		5009	*S. griseoplanus*		
		5555	*S. libani*		
		5461	*S. lydicus*		
		5357	'*S. natalensis*'		
		5276	*S. nigrescens*		
		5241	'*S. saraceticus*'		
		5032	'*S. sioyaensis*'		
29B	*S. lydicus*	5492	*S. albulus*		
		5030	'*S. toyocaensis*'		
30	*S. filipinensis*	5107	*S. curacoi*	18	*S. cyaneus*
31A	*S. antibioticus*	5234	*S. antibioticus*	31	*S. antibioticus*
		5367	*S. phaeofaciens*		
31B	*S. antibioticus*	5317	*S. lucensis*		
		5306	*S. misionensis*		
		5282	*S. naganishii*		
40	*S. phaeochromogenes*	5594	*Chainia ochrea*	41	*C. ochrea*
		5048	*S. parvullus*	12	*S. rochei*
42	*S. rimosus*	5268	*S. albofaciens*	42	*S. rimosus* (Cluster-group B)
		5535	*S. anandii*		
		5402	'*S. capuensis*'		
		5545	*S. chrestomyceticus*		
		5366	'*S. flavofungini*'		
		5500	*S. kanamyceticus*		
		5260	*S. rimosus*		
44	*S. pactum*	5345	'*S. karnatakensis*'	44	*S. pactum* (Cluster-group C)
		5530	*S. pactum*		
62	*S. luridus*	5479	*S. cirratus*	62	*S. luridus* (Cluster-group F)
		5431	*S. helvaticus*		
Single member clusters					
		M673	'*Kitasatoa antimyceticus*'	8	'*S. alni*'
		N745	*Saccharopolyspora hirsuta*	41	*Chainia ochracea*
		5028	*S. achromogenes*	19	*S. diastaticus*
		5557	'*S. alni*'	8	'*S. alni*'
		5139	*S. badius*	SMC	Cluster-group C
		5564	*S. bluensis*	39	*S. longisporoflavus*
		5017	*S. canus*	25	*S. canus*
		5061	*S. flaveolus*	24	*S. flaveolus*
		5480	*S. galbus*	43	*S. griseoluteus*
		5456	*S. griseoflavus*	37	*S. griseoflavus*
		5392	*S. griseoluteus*	43	*S. griseoluteus*
		5081	*S. luridus*	62	*S. luridus*

Table 8 (*continued*)

S_J assignment				S_{SM} assignment	
Cluster no.	Designation of cluster	Strain no.	Strain name	Cluster no.*	Name of cluster
		5096	'*S. macrosporeus*'	38	*S. prasinosporus*
		5553	*S. mirabilis*	19	*S. diastaticus*
		5026	*S. pseudogriseolus*	12	*S. rochei*
		5547	'*S. steffisburgensis*'	38	*S. prasinosporus*
		5365	'*S. thermophilus*'	15	*S. chromofuscus*
		A84	'Cluster A'	49	'Cluster A/B'
		A53	'Cluster B'		
New clusters					
1		5043	*S. alboniger*	1B	*S. albidoflavus*
		5386	*S. aureocirculatus*	3	*S. atroolivaceus*
		5136	*S. albovinaceus*	1B	*S. albidoflavus*
		5019	*S. pluricolorescens*		
2		5127	*S. aureofaciens*	14	*S. aureofaciens*
		5324	*S. gougerotii*	1A	*S. albidoflavus*
		5258	*S. catenulae*	43	*S. griseoluteus*
		5100	*S. ramulosus*	SMC	Cluster-group C
3		5561	'*S. cretaceus*'	3	*S. atroolivaceus*
		5321	'*S. krainskii*'	1A	*S. albidoflavus*
		5275	*S. griseoruber*	21	*S. griseoruber*
		5281	*S. griseoruber*		
4		5568	*S. lusitanus*	44	*S. pactum*
		5566	'*S. pulcher*'	12	*S. rochei*
CLUSTER-GROUP E					
52	*N. asteroides*	N317	*N. asteroides*	52	*Nocardia* spp. (Cluster-group E)
		5040	'*N.' orientalis*		
53	'*N.' mediterranea*	N730	'*N.' mediterranea*	53	'*N.' mediterranea* (Cluster-group E)
		N731	'*N.' mediterranea*		
		N732	'*N.' mediterranea*		
		N733	'*N.' mediterranea*		
		5501	'*S.' mediterranei*		
		N737	'*S.' tolypophorus*		
		N738	'*S.' tolypophorus*		
		N734	*Streptomyces* sp.		
54	'*S. aureofasciculus*'	5414	'*S. aureofasciculus*'	54	*S. alboflavus* (Cluster-group E)
		5435	'*S. longissimus*'		
CLUSTER-GROUP F1					
55A	*Stv. griseocarneum*	5004	*Stv. griseocarneum*	55	*Stv. griseocarneum* (Cluster group F)
		5038	*Stv. luteoverticillatum*		
55B	*Stv. griseocarneum*	5520	'*S. tropicalensis*'		
		5005	*Stv. cinnamoneum*		
		5114	*Stv. hachijoense*		
		5221	*Stv. mashuense*		
55C	*Stv. griseocarneum*	5315	'*S. paucisporogenes*'		
		5577	*Stv. septatum*		
		5436	*Stv. rectiverticillatum*	57	*Stv. hiroshimense*
56	*Stv. netropsis*	5526	*S. avidinii*	56	*Stv. netropsis* (Cluster-group F)
		5604	*S. eurocidicum*		
		5093	*Stv. flavopersicum*		
		5259	*Stv. netropsis*		
58	*Stv. blastmyceticum*	5603	'*S. caespitosus*'	58	*Stv. blastmyceticum* (Cluster-group F)
		5029	*Stv. blastmyceticum*		

Table 8 (*continued*)

S_J assignment				S_{SM} assignment	
Cluster no.	Designation of cluster	Strain no.	Strain name	Cluster no.*	Name of cluster
Single member clusters					
		5503	'*S. moro-okaensis*'	59	*Stv. biverticillatum*
		5565	'*S. aspergilloides*'		
		5051	*Stv. albireticuli*	SMC	Cluster-group F
		M636	*Stv. baldaccii*	SMC	
		5507	*Stv. griseoverticillatum*	58	*Stv. blastmyceticum*
		5052	*Stv. kentuckense*	SMC	Cluster-group F
		5587	*Stv. ladakanum*	SMC	
		M640	*Stv. luteoverticillatum*	55	*Stv. griseocarneum*
		M638	*Stv. mobaraensis*	58	*Stv. blastmyceticum*
New Cluster					
		M635	*Stv. biverticillatum*	59	*Stv. biverticillatum*
		5037	*Stv. hiroshimense*	57	*Stv. hiroshimense*
CLUSTER-GROUP F2					
61A	*S. lavendulae*	5558	*S. colombiensis*	61	*S. lavendulae* (Cluster-group F)
		5190	*S. goshikiensis*		
		5069	*S. lavendulae*		
		5445	*S. subrutilus*		
61B	*S. lavendulae*	5152	*S. flavotricini*		
		5178	*S. toxytricini*		
61C	*S. lavendulae*	5550	*S. katrae*		
		5316	*S. polychromogenes*		
		5194	*S. racemochromogenes*		
61D	*S. lavendulae*	5216	*S. lavendulocolor*	5	*S. exfoliatus*
		5175	*S. roseoviridis*		
66	*S. misakiensis*	5222	*S. misakiensis*	66	*S. misakiensis* (Cluster-group F)
		5239	'*S. viridifaciens*'		
		5575	*S. xanthocidicus*		
Single member clusters					
		5570	*S. albolongus*	63	*S. xanthochromogenes*
		5581	*S. bikiniensis*	64	*S. bikiniensis*
		5222	*S. misakiensis*	66	*S. misakiensis*
		5511	'*S. ostreogriseus*'	25	*S. canus*
		5094	*S. virginiae*	61	*S. lavendulae*
		5111	*S. xanthochromogenes*	63	*S. xanthochromogenes*
		5134	*S. xanthophaeus*	61	*S. lavendulae*
		F6	*Streptomyces* sp.	63	*S. xanthochromogenes*
		SW1	*Streptomyces* sp.	64	*S. bikiniensis*
CLUSTER-GROUP F3					
65	*Kitasatoa* spp.	Ka280	*K. diplospora*	65	*Kitasatoa* spp. (Cluster-group F)
		Ka281	*K. kauiensis*		
		Ka282	*K. nagasakiensis*		
		Ka279	*K. purpurea*		
		5244	*S. xantholiticus*	24	*S. flaveolus*
SINGLE MEMBER CLUSTER-GROUPS					
		A5	*Actinomadura helvata*	SMC	Cluster-group E
		IC	*Intrasporangium calvum*	SMC	Cluster-group J
		N950	*Nocardioides albus*	SMC	Cluster-group A
		5197	'*S. albocyaneus*'	SMC	Cluster-group A
		5219	*S. amakusaensis*	SMC	Cluster-group B
		5141	*S. candidus*	3	*S. atroolivaceus*
		5218	*S. finlayi*	SMC	Cluster-group I

Table 8 (*continued*)

S_J assignment				S_{SM} assignment	
Cluster no.	Designation of cluster	Strain no.	Strain name	Cluster no.*	Name of cluster
		5065	*S. gelaticus*	SMC	Cluster-group A
		5398	'*S. luteofluorescens*'	SMC	Cluster-group J
		5035	*S. massasporeus*	SMC	Cluster-group D
		5021	'*S. mediocidicus*'	SMC	Cluster-group F
		5358	*S. novaecaesareae*	SMC	Cluster-group J
		5041	*S. platensis*	29	*S. lydicus*
		5506	*S. prasinosporus*	38	*S. prasinosporus*
		5335	*S. prunicolor*	11	*S. prunicolor*
		A28	'*S. somaliensis*'	70	'*S. viridoflavus*'
		5237	'*S. viridoflavus*'		
		5104	*S. sulphureus*	SMC	Cluster-group C
		5571	*Stv. orinoci*	58	*Stv. blastmyceticum*
		5027	*Stv. thioluteum*	SMC	Cluster-group F
		A46	'Cluster B'	70	'*S. viridoflavus*'
NEW CLUSTER-GROUPS					
1		G5	'*S. lactamdurans*'	7	'*S. roseus*'
		G6	*S. lipmanii*		
		5076	'*S. roseus*'		
2		A16	*A. madurae*	50	*Actinomadura* spp.
		A17	*A. madurae*		
		A3	*A. pusilla*		
		A2	*A. roseoviolacea*		
3		A4	*A. verrucosospora*		
		E63	*Microtetraspora glauca*		
4		5002	*S. chattanoogensis*	35	*S. chattanoogensis*
		5109	*S. nodosus*		
5		5574	'*S. thermoflavus*'	36	*S. thermovulgaris*
		5579	*S. thermonitrificans*		
		5444	*S. thermovulgaris*		
6		HR1	Acidophilic soil isolates	72	Acidophilic isolates
		MR2			
		SW10			
7		MR22	Acidophilic soil isolates		
		SW5			
8		5412	*S. aurantiacus*	45	*S. aurantiacus*
		5494	*S. capoamus*		
		5443	*S. thermoviolaceus*		
9		5567	'*S. paraguayensis*'	46	*S. varsoviensis*
		5346	*S. varsoviensis*		
		5104	*S. sulphureus*	SMC	Cluster-group C
10		A19	*A. pelletieri*	73	*A. pelletieri*
		A20	*A. pelletieri*		
11		5011	'*N.*' *autotrophica*	69	'*Nocardia*' spp.
		5472	'*N. salmonicida*'		
12		5554	*S. avellaneus*	67	*S. psammoticus*
		5341	*S. psammoticus*		
13		G1	'*S. cattleya*'	47	*S. tubercidicus*
		5261	*S. tubercidicus*		
14		G2	*S. clavuligerus*	71	*S. clavuligerus*
		G4	'*S. jumonjinensis*'		
15		5024	'*S. pyridomyceticus*'	48	'*S. pyridomyceticus*'
		A87	'Cluster A'		
16		MR10	Acidophilic soil isolates	51	Acidophilic isolates
		MR19	Acidophilic soil isolates		

* SMC, single member cluster.

the second subcluster. Clusters 15 (*S. chromofuscus*) and 55 (*Stv. griseocarneum*) were each recovered as three related subclusters, whereas cluster 61 (*S. lavendulae*) strains fell into four allied clusters and those of cluster 19 (*S. diastaticus*) into five less well related taxa (Table 8).

In the case of the minor phena, clusters 4 (*Nocardiopsis dassonvillei*), 7 ('*S. roseus*'), 9 (*S. californicus*), 13 (*S. cellulosae*), 22 ('*Chainia*' *poonensis*), 26 (*S. graminofaciens*) 27 (*S. viridochromogenes*), 28 (*S. glaucescens*), 33 ('*S. chromogenus*'), 56 (*Stv. netropsis*), 60 (*Stv. griseostramineus*) and 65 (*Kitasatoa* spp.) were recovered above the 63% *S*-level. Clusters 35 (*S. chattanoogensis*), 36 (*S. thermovulgaris*), 45 (*S. aurantiacus*), 46 (*S. varsoviensis*), 47 (*S. tubercidicus*), 48 (*S. pyridomyceticus*), 49 (cluster A/B), 51 (acidophilic isolates), 52 (*Nocardia* spp.), 54 (*S. alboflavus*), 63 (*S. xanthochromogenes*), 64 (*S. bikiniensis*), 66 (*S. misakiensis*), 67 (*S. psammoticus*), 68 (*S. fradiae*), 69 ('*Nocardia*' spp.) 71 (*S. clavuligerus*), 72 (*acidophilic isolates*), 73 (*Actinomadura pelletieri*) were recognized as distinct taxa below this similarity level. Of the remaining minor phena, clusters 23 (*S. microflavus*), 30 (*S. filipinensis*), 34 (*S. nogalater*), 39 (*S. longisporoflavus*), 44 (*S. pactum*), 58 (*Stv. blastmyceticum*), 62 (*S. luridus*) and 70 ('*S. viridoflavus*') were recovered but altered in composition. Clusters 2 ('*Stv.*' *olivoverticillatum*), 8 ('*S. alni*') 11 (*S. prunicolor*), 14 (*S. aureofaciens*), 24 (*S. flaveolus*), 25 (*S. canus*), 38 (*S. prasinosporus*), 41 (*Chainia ochracea*), 43 (*S. griseoluteus*), 57 (*Stv. hiroshimense*) and 59 (*Stv. biverticillatum*) were no longer recognizable.

DISCUSSION

Numerical taxonomy is of value for both classification and identification. The phena defined are polythetic, so no single character is either indispensable or sufficient to entitle an organism to group membership. The principles of numerical taxonomy are, therefore, in sharp contrast to the traditional approaches to streptomycete taxonomy which have usually involved recognition of taxa on the basis of a few subjectively chosen characters (e.g. Gause *et al.*, 1957; Pridham *et al.*, 1958; Hütter, 1967; Pridham & Tresner, 1974*b*; Pridham, 1976; Szabo & Marton, 1976).

Nevertheless, the results of numerical phenetic studies must be interpreted carefully, as similarities between strains can be distorted by test and sampling error, low test reproducibility and the choice of statistical analyses (Sneath & Johnson, 1972; Austin & Colwell, 1977; Goodfellow *et al.*, 1979). Studies which include a diversity of taxa can present special problems due to the difficulty in defining standard conditions which are suitable for the good growth of all test strains. This can lead to the construction of phena which are artefacts. However, the quality of the test data can be assessed by estimating test error (Sneath & Johnson, 1972), determining the contents and relationships of clusters defined by different statistical procedures (Austin & Colwell, 1977), assessing cluster overlap (Sneath, 1977, 1979) and by comparing the results of numerical classifications with those based on chemical, genetical and serological criteria (Sneath, 1976; Jones & Sackin, 1980; Piot *et al.*, 1980; Goodfellow & Wayne, 1982). Thus, chemical and nucleic acid pairing studies have assisted in the interpretation of numerical phenetic classifications of several actinomycete taxa (Lechevalier & Lechevalier, 1970*a*, *b*; Lechevalier *et al.*, 1977; Minnikin & Goodfellow, 1976, 1978, 1980, 1981; Bradley & Mordarski, 1976; Bradley, 1980; Mordarski *et al.*, 1980*a*, *b*, 1981).

In the present investigation, the taxonomic groupings were not markedly affected by test error (p) which was low at 3·36%. This experimental error compares favourably with that from similar investigations on facultatively anaerobic actinomycetes (p 3·12%, Holmberg & Nord, 1975; p 1·6%, Schofield & Schaal, 1981), actinomaduras (p 4·5%, Goodfellow *et al.*, 1979), rhodococci (p 3·7%, Goodfellow & Alderson, 1977), sporactinomycetes containing *meso*-DAP in the wall peptidoglycan (p 2·1%, Goodfellow & Pirouz, 1982) and *Nocardia amarae* (p 1·5%, Goodfellow *et al.*, 1982). It was also well within the 10% limit suggested by Sneath & Johnson (1972).

Most of the major clusters defined in the S_{SM} analysis showed little significant overlap (taking 5% as the expected level), which was encouraging in view of the difficulties experienced in distinguishing streptomycete taxa in some earlier numerical phenetic studies (Gyllenberg, 1970; Gyllenberg *et al.*, 1967; Paszkiewicz, 1972). This suggests that some of the diffuse and over-

lapping clusters recovered in the earlier analyses were due to their narrow data base and the poor quality of some tests used.

The value of 5% used here for expected overlap, although not stringent, is less than that of about 8·3% which corresponds to continuous variation (Sneath, 1977). It would be unrealistic to demand very low values of overlap in the present state of streptomycete taxonomy, as species definition and variation will need further clarification. The pattern may represent partially overlapping variation rather than sharply defined, well separated species.

Some of the overlap found between *S. albidoflavus* (cluster 1) and *S. chromofuscus* (cluster 15), *S. exfoliatus* (cluster 5), *S. griseoviridis* (cluster 17), *S. rimosus* (cluster 42), *S. violaceus* (cluster 6) and '*N.*' *mediterranea* (cluster 53) may reflect the inadequacies of some of the tests employed in the present analysis. Alternatively, *S. albidoflavus* may represent a diffuse cluster in phenetic hyperspace around which some of the other major clusters congregate. However, the considerable overlap of clusters 5 and 6 may indicate that they represent one cluster.

The groupings provided by the S_{SM} and S_J coefficients were derived from characteristics which were determined in conditions that were generally conducive to growth of streptomycetes. The composition and relationships of taxa containing other genera, and in some cases those including streptomycetes, were inevitably influenced by an excess of negative matches. Thus *Streptoverticillium* (clusters 55–59), *Kitasatoa* (cluster 65) and *S. lavendulae* (cluster 61) strains formed distinct cluster-groups in the S_J analysis, but their relative lack of activity in many of the tests was primarily responsible for their recovery in cluster-group F in the S_{SM} study. Similarly, *Actinomadura* (cluster 50) and '*N.*' *mediterranea* (cluster 53) strains formed distinct cluster-groups in the S_J analysis but were an integral part of cluster-group E when negative matches were taken into account. The inconsistent positions of some of the marker strains can also be attributed to their poor and/or slow growth on some of the test media. It is also evident that the strains assigned to cluster 43 (*S. griseoluteus*), 44 (*S. pactum*), 45 (*S. aurantiacus*), 46 (*S. varsoviensis*) and 47 (*S. tubercidicus*) were classified in cluster-group C due to their poor growth on many of the test media. However, most of the larger *Streptomyces* clusters defined by the S_{SM} coefficient were not substantially changed by the S_J analysis.

The delineation of cluster-groups at the 70·1% (S_{SM}) and 50% (S_J) *S*-levels was useful, but to some extent, arbitrary. In each analysis, however, the vast majority (>71%) of the test strains fell into cluster-group A, which could, therefore, be roughly equated with the genus *Streptomyces* (Williams *et al.*, 1981). Some streptomycete strains were placed into this cluster-group by S_J but not by S_{SM} analysis. These included *S. rimosus* (cluster 42), *S. pactum* (cluster 44), *S. alboflavus* (cluster 54) and *Stv. griseostramineus* (cluster 60). The converse applied to *S. chattanoogensis* (cluster 35) and *S. thermovulgaris* (cluster 36). There seems to be no reason to doubt the generic status of such strains. Thirty-seven other *Streptomyces* strains consistently fell outside cluster-group A. These included the major cluster *S. lavendulae* (cluster 61) and the minor clusters 45 (*S. aurantiacus*), 46 (*S. varsoviensis*), 47 (*S. tubercidicus*), 63 (*S. xanthochromogenes*), 66 (*S. misakiensis*), 67 (*S. psammoticus*), 68 (*S. fradiae*) and 71 (*S. clavuligerus*), together with six unclustered strains. The generic status of these strains is less certain, but it is likely that most of them were excluded from cluster-group A due to their relative lack of activity on many of the test media. Most of them have a wall chemotype I (Pridham & Lyons, 1969; Shirling & Gottlieb, 1976), and produce long chains of spores on their aerial hyphae (Shirling & Gottlieb, 1968*a*, 1969, 1972); some of them, such as *S. lavendulae* ISP 5069, are lysed by phage virulent for *Streptomyces* (Prauser, 1976*b*). The acidophilic isolates were distinct from all of the neutrophilic streptomycetes, confirming the results of Williams & Khan (1974) and Khan & Williams (1975). As all tests were performed at a lower pH than that used for other strains, the results must be viewed with caution; the taxonomic status of these strains requires further investigation.

The distribution of the various genera representatives relative to the *Streptomyces* cluster-group A was summarized by Williams *et al.* (1981). Marker strains of most of the genera with a wall chemotype I were unambiguously assigned to the '*Streptomyces*' cluster-group. These strains include all of the representatives of the genera *Actinopycnidium*, *Actinosporangium*, *Chainia*, *Elytrosporangium* and *Microellobosporia*, though *Microellobosporia violacea* M297 was recovered in cluster-group D in the S_{SM} analysis. The classification of the *Chainia* strains within

the *Streptomyces* cluster-group agrees with the results from other studies (Gattani, 1957; Becker *et al.*, 1965; Hütter, 1965; Lechevalier & Lechevalier, 1965; Pridham, 1970; Pridham & Tresner, 1974*b*; Kroppenstedt *et al.*, 1981) and clearly shows that the ability to form sclerotia (Thirumalachar, 1955) is not a genus specific property. Similarly, the overall affinity evident between strains of *Actinopycnidium*, *Actinosporangium*, *Elytrosporangium*, *Microellobosporia* and *Streptomyces* outweighs the reported morphological differences found between them (Krasilnikov & Yuan, 1961; Krasilnikov, 1962; Cross *et al.*, 1963; Falcao de Morais *et al.*, 1966; Cross & Al-Diwany, 1981). In addition, strains of these taxa are susceptible to polyvalent *Streptomyces* phages (Prauser *et al.*, 1967; Prauser & Falta, 1968; Prauser, 1976*b*; Wellington & Williams, 1981). They also have G plus C ratios (Tsyganov *et al.*, 1966; Yamaguchi, 1967; Monson *et al.*, 1969; Farina & Bradley, 1970) and chemical properties (Lechevalier & Lechevalier, 1970*b*; Dunphy *et al.*, 1971; Collins *et al.*, 1977, 1980; Lechevalier *et al.*, 1977; Minnikin & Goodfellow, 1981) in common with streptomycetes and share a high DNA homology with the latter (Monson *et al.*, 1969; Kroppenstedt *et al.*, 1981). Therefore, data from chemical, genetical, phage host range and numerical phenetic studies show that *Actinopycnidium*, *Actinosporangium*, *Chainia*, *Elytrosporangium* and *Microellobosporia* are synonyms of *Streptomyces*. Strains of *Nocardioides*, *Nocardiopsis* and *Saccharopolyspora* were also associated with the *Streptomyces* cluster-group. *Nocardioides albus* N950 (wall chemotype I) was loosely associated with cluster group A in the S_{SM} analysis but formed a separate single member cluster-group with the S_J coefficient. This organism produces a mycelium which fragments into rod- and coccus-like elements, and is resistant to phage virulent to *Streptomyces* and related genera (Prauser, 1976*a*, *b*; Wellington & Williams, 1981). It can also be distinguished from streptomycetes by DNA–DNA pairing (Tille *et al.*, 1978) and lipid analyses (Lechevalier *et al.*, 1977). *Nocardioides* therefore merits generic status.

Saccharopolyspora hirsuta N745 (wall chemotype IV) also formed a loose association with cluster-group A. It differs from *Streptomyces* in its wall chemotype (Lacey & Goodfellow, 1975) and its resistance to streptomycete phages (Wellington & Williams, 1981). Its taxonomic position, and particularly its relationship to *Micropolyspora faeni* (Goodfellow & Minnikin, 1981) therefore requires further study.

The sharp separation of *Nocardiopsis* (*Actinomadura*) *dassonvillei* (wall chemotype III) (cluster 4) from *Actinomadura madurae* (cluster 50) and *Actinomadura pelletieri* (cluster 73) is in agreement with other recent studies (Lechevalier & Gerber, 1970; Lechevalier *et al.*, 1971, 1977; Agre *et al.*, 1975; Williams *et al.*, 1976; Collins *et al.*, 1977; Minnikin *et al.*, 1977; Yamada *et al.*, 1977; Lacey *et al.*, 1978; Minnikin & Goodfellow, 1978; Goodfellow & Minnikin, 1981) and with data from more extensive numerical phenetic surveys (Tsukamura, 1969; Goodfellow, 1971; Alderson & Goodfellow, 1979; Goodfellow *et al.*, 1979; Goodfellow & Pirouz, 1982). However, the unambiguous classification of *Nocardiopsis dassonvillei* with the streptomycetes of cluster-group A is puzzling, though it has been found previously to resemble *S. griseus* phenetically (Gordon & Horan, 1968*b*). *Nocardiopsis* can be distinguished from *Streptomyces* on the basis of wall (Lechevalier & Lechevalier, 1970*a*, *b*) and lipid composition (Collins *et al.*, 1977; Lechevalier *et al.*, 1977; Minnikin & Goodfellow, 1978) and in its reactions to phage (Wellington & Williams, 1981). It has also been found to be phylogenetically distinct from *Streptomyces* and related taxa in rRNA oligonucleotide catalogue data (Stackebrandt & Woese, 1981).

The representatives of three of the remaining genera with a wall chemotype I, *Intrasporangium*, *Kitasatoa* and *Streptoverticillium*, were not classified in the *Streptomyces* cluster-group in either the S_{SM} or S_J analysis. *Intrasporangium calvum* IC was negative for most of the tests and shared little similarity with any of the other strains. It has been distinguished from streptomycetes on the basis of lipid composition (Lechevalier *et al.*, 1977) and is resistant to *Streptomyces* phages (Prauser & Falta, 1968; Wellington & Williams, 1981). Further strains of *Intrasporangium* need to be isolated to determine its status and affinities. The *Kitasatoa* and *Streptoverticillium* strains were more reactive, formed distinct cluster-groups in the S_J analysis and were recovered in cluster-group F, together with *S. lavendulae*, in the S_{SM} run. Streptoverticillia formed a distinctive phenon in the earlier numerical phenetic studies on strepto-

mycetes and related strains (Silvestri *et al.*, 1962; Kuryłowicz *et al.*, 1975, 1976), while *S. lavendulae* ISP 5069 was shown to have a high overall similarity with streptoverticillia by Silvestri *et al.* (1962).

In the S_{SM} analysis, the streptoverticillia were assigned to five clusters with four single member clusters which included *Stv. baldacci* M626, the type species of the genus. Strains received as '*S. aspergilloides*' ISP 5565, '*S. caespitosus*' ISP 5603, '*S. moro-okaensis*' ISP 5503, '*S. paucisporogenes*' ISP 5315 and '*S. tropicalensis*' ISP 5520 were again found to produce verticillate sporophores (Shirling & Gottlieb, 1969, 1972) and clustered with the streptoverticillia. Most of these strains were also classified with streptoverticillia in the numerical phenetic studies of Kuryłowicz *et al.* (1975, 1976). With the S_J analysis, 15 of the 23 streptoverticillia remained in the same clusters. A *Streptoverticillium* cluster-group (F1) was defined which included all strains except for *Stv. orinoci* ISP 5571 and *Stv. thioluteum* ISP 5027 which formed cluster-groups of their own.

Despite the phenetic distinctions between streptoverticillia and streptomycetes, it is clear that the two genera are closely related. Thus, strains from each genus have a wall chemotype I (Lechevalier & Lechevalier, 1970*a*, *b*) and DNA rich in G plus C (Pridham & Tresner, 1974*a*), share high DNA homology values (Okanishi & Gregory, 1970; Okanishi *et al.*, 1972; Toyama *et al.*, 1974; Kroppenstedt *et al.*, 1981), and are attacked by the same phages (Prauser, 1976*b*; Wellington & Williams, 1981). They also have comparable menaquinones (Dunphy *et al.*, 1971; Collins *et al.*, 1977, 1980), fatty acids and polar lipids (Kroppenstedt & Kutzner, 1976; Lechevalier *et al.*, 1977). The continued recognition of the genus *Streptoverticillium* as a taxon related to, but distinguishable from, *Streptomyces* is nevertheless a practical proposition.

However, the practice of grouping streptoverticillium species on the basis of the colour of their spore mass and substrate mycelium (Locci *et al.*, 1969; Baldacci & Locci, 1974) is not supported by our results. Further studies on more strains are needed to amplify that of Konev & Mitnitskii (1980) and to define criteria for the characterization of *Streptoverticillium* species.

The genus *Kitasatoa* was classified in the family *Actinoplanaceae* (Matsumae & Hata, 1968) on the basis of its ability to produce motile spores in spore vesicles, but Cross & Goodfellow (1973) transferred it to the family *Streptomycetaceae*. Subsequent studies have clearly shown that all four recognized species of *Kitasatoa* (Skerman *et al.*, 1980) share many properties with streptomycetes and related strains. Thus, kitasatoas have a wall chemotype I and phospholipids similar to those of streptomycetes (Lechevalier *et al.*, 1977; Hasegawa *et al.*, 1979; Kutzner, 1981), are lysed by phage virulent for streptomycetes (Wellington & Williams, 1981), share a relatively high DNA homology with *Actinosporangium*, *Elytrosporangium*, *Microellobosporia* and *Streptomyces* strains (Kroppenstedt *et al.*, 1981), and are phylogenetically close to the latter (Stackebrandt & Woese, 1981; Stackebrandt *et al.*, 1981). In the present study, the four recognized *Kitasatoa* species formed a homogeneous taxon, produced RF chains of spores but did not form spore vesicles. These data are strongly supported by those from DNA–DNA pairing studies (Kroppenstedt *et al.*, 1981) which show that *K. diplospora*, *K. kauaiensis*, *K. nagasakiensis* and *K. purpurea* are genetically identical. The chemical, genetical and numerical phenetic data provide sufficient grounds for reducing *K. diplospora*, *K. kauaiensis* and *K. nagasakiensis* to synonyms of *K. purpurea*, and transferring this species to the genus *Streptomyces*.

'*Kitasatoa antimyceticus*' (M673), which is not cited in the *Approved Lists of Bacterial Names* (Skerman *et al.*, 1980), was recovered in the *Streptomyces* cluster-group in both the S_{SM} and S_J analysis, sharing a high affinity with '*S. alni*' ISP 5557. This organism is also lysed by *Streptomyces* phages (Wellington & Williams, 1981) and is clearly a streptomycete.

Apart from *Nocardiopsis dassonvillei* and *Saccharopolyspora hirsuta*, the marker strains which had a wall chemotype other than I were not recovered in the *Streptomyces* cluster-group A. Thus, strains of *Actinomadura sensu stricto* (Goodfellow *et al.*, 1979), which have a wall chemotype III and contain madurose (Lechevalier & Lechevalier, 1970*a*, *b*), were clearly distinguished from cluster-group A. The loose association found between *A. madurae* A16 and A17, *A. helvata* A5, *A. pusilla* A3, *A. roseoviolacea* A2, *A. verrucosospora* A4 and *Microtetraspora glauca* E63, and their sharp separation from *A. pelletieri* (cluster 73) agrees with the results of Alderson &

Goodfellow (1979), Goodfellow *et al.* (1979) and Goodfellow & Pirouz (1982), as does the high similarity between *A. pelletieri* A19 and A20 and *S. somaliensis* A28 in the S_{SM}, as opposed to the S_J, analysis. However, *S. somaliensis* strains, like other streptomycetes, have a wall chemotype I, and can readily be distinguished from *A. pelletieri* with a wall chemotype III (Becker *et al.*, 1965; Pridham & Lyons, 1969; Lechevalier & Lechevalier, 1970*a*, *b*). The lipids of *S. somaliensis* are also similar to those of other streptomycetes (Lechevalier *et al.*, 1977; Minnikin *et al.*, 1977).

Marker strains received as *Nocardia* also fell outside cluster-group A, although they did not all fall into the same cluster group. It is not relevant here to dwell on the inter-relationships of these strains, which have been considered in detail elsewhere (Mordarska *et al.*, 1972; Goodfellow & Minnikin, 1977, 1978, 1981; Goodfellow & Schaal, 1979; Goodfellow *et al.*, 1979; Minnikin & Goodfellow, 1980, 1981; Orchard & Goodfellow, 1980). However, it is worth noting that '*Nocardia capreola*' ISP 5225 was clearly distinguished from all of the strains studied. It was reported to contain *meso*-DAP with traces of arabinose and galactose (Pridham & Lyons, 1969) and requires further study.

The recovery of '*Nocardia*' *mediterranea* and '*S. tolypophorus*' strains in a cluster separated from both the *Streptomyces* cluster-group and from *N. asteroides* N317 is consistent with the findings of previous investigations. '*Nocardia*' *mediterranea* and '*S. tolypophorus*' can be excluded from the genus *Streptomyces* by chemical, numerical, phenetic, morphological and phage host range studies (Pridham & Lyons, 1969; Thiemann *et al.*, 1969; Shibata *et al.*, 1971; Kroppenstedt & Kutzner, 1978; Alderson *et al.*, 1981; Wellington & Williams, 1981) and from *Nocardia sensu stricto* by detailed peptidoglycan structure, absence of mycolic acids and lipid composition (Bordet *et al.*, 1972; Pommier & Michel, 1973; Lederer *et al.*, 1975; Alderson *et al.*, 1981). Comparative studies on representatives of all taxa with a wall chemotype IV which lack mycolic acids are needed to clarify the taxonomic status and affinities of '*N.*' *mediterranea*.

The main aim of this study was to provide an objective basis for the classification of the large number of *Streptomyces* species described. The results indicated that most *Streptomyces* strains fell into 18 major centres of variation, distinct from the *Actinomadura*, '*Nocardia*' *mediterranea* and *Streptoverticillium* major clusters, or into a number of minor clusters. These results indicate that streptomycetes have been grossly overclassified. This conclusion is supported by previous numerical phenetic studies (Gilardi *et al.*, 1960; Silvestri *et al.*, 1962; Gyllenberg *et al.*, 1967; Kuryłowicz *et al.*, 1969, 1975, 1976; Gyllenberg, 1970, 1974; Paszkiewicz, 1972; Szulga, 1978), by other phenetic studies (Hütter, 1967; Gordon, 1968; Gordon & Horan, 1968*a*; Korn *et al.*, 1978), and by DNA–DNA pairing data (Tewfik & Bradley, 1967; Okanishi & Gregory, 1970; Okanishi *et al.*, 1972; Toyama *et al.*, 1974).

Some of the major clusters defined, such as clusters 3 (*S. atroolivaceus*), 16 (*S. albus*), 17 (*S. griseoviridis*) and 32 (*S. violaceoniger*), were consistent and relatively homogeneous. Others, like clusters 5 (*S. exofoliatus*), 15 (*S. chromofuscus*), 19 (*S. diastaticus*) and 20 (*S. olivaceoviridis*), were recovered as two or more phena in the S_J analysis. There was also evidence of overlap between some of the major clusters. It is, therefore, appropriate to regard the more heterogeneous major clusters as species-groups rather than species, pending the results of current studies on their genetical and chemical relationships. However, some major and most minor clusters could be regarded as species.

Comparison of the clusters defined with previous groupings of streptomycetes is impeded to some extent by the inconsistent choices of strains and tests. Nevertheless, some useful parallels can be drawn. The 43 species-groups, containing 463 species, compiled by Pridham & Tresner (1974*b*) in the eighth edition of *Bergey's Manual of Determinative Bacteriology*, were based on four characters. The states of these characters throughout the major streptomycete clusters are summarized in Table 9. Some clusters, such as *S. albidoflavus*, *S. albus*, *S. violaceoniger* and *S. lavendulae*, were reasonably consistent in these character states, while others, such as *S. violaceus*, *S. chromofuscus* and *S. diastaticus*, were not. It was also notable that strains with the same character states could fall into different clusters (e.g. *S. olivaceoviridis*, *S. griseoruber* and *S. lydicus*). It is not surprising that polythetic groups defined by 139 characters do not always show concordance with those constructed using four subjectively chosen characters.

Streptomyces albidoflavus, divisible into three sub-clusters, was the largest cluster and can be

approximately equated with the '*griseus*' groups recognized previously (Baldacci & Comaschi, 1956; Ettlinger *et al.*, 1958; Kutzner & Waksman, 1959; Waksman, 1959; Silvestri *et al.*, 1962; Hütter, 1963; Pridham, 1963–1964; Lyons & Pridham, 1966; Gyllenberg *et al.*, 1967; Wóznika, 1967; Gordon & Horan, 1968*a*; Kuryłowicz *et al.*, 1969). The *S. albidoflavus* cluster also corresponds to phenon XII, and groups E_1 and E_2, defined by Kuryłowicz *et al.* (1975, 1976) using the so-called Wrocław taxonomy and centrifugal correlation statistics, respectively. The phena defined in these taxometric studies do, however, also include organisms assigned to a number of diverse clusters in the present study. For example, the two largest phena, E_1 and XII, in addition to containing *S. albidoflavus*-like organisms, also include strains assigned to clusters 15 and 20, respectively, in the present study. It is also interesting that some of the characteristics of the cluster 1 isolates are similar to those listed for the *S. griseus* group by earlier workers (Lyons & Pridham, 1966; Gordon & Horan, 1968*a*). These include the formation of smooth spores in RF chains, the utilization of L-arabinose, L-fructose, D-xylose and citrate as sole carbon compounds, the lack of melanin pigments, and the ability to degrade adenine, casein, hypoxanthine, starch, L-tyrosine, urea and xanthine.

The compositions of the three subclusters of cluster 1 are also comparable with the results of some earlier investigations. All of the subcluster 1A (*S. coelicolor*) species, except *S. craterifer*, were considered to be synonyms of *S. coelicolor* ISP 5233 by Korn *et al.* (1978) on the basis of ISP data and the studies of Kutzner *et al.* (1978), while Silvestri *et al.* (1962) found that *S. coelicolor* ISP 5233, *S. intermedius* ISP 5372 and *S. rutgersensis* ISP 5077 were an integral component of sphere XVII. Ten of the subcluster 1A strains were recovered in group E_2, together with *S. coelicolor* ISP 5233, by Kuryłowicz *et al.* (1975, 1976).

Over half of the ISP strains in subcluster 1B (*S. griseus*) were classified in the *S. griseus* group of Korn *et al.* (1978); these included *S. ornatus* ISP 5307 which shared over 92% S_{SM} with *S. griseus* ISP 5326. In addition, 18 subcluster 1B strains were listed in the specific epithets regarded as synonyms of *S. griseus* by Hütter (1967). However, only four of ten species tentatively regarded as sub-species of *S. griseus* by Pridham (1963–1964) were recovered in the subcluster; the others were classified in subclusters 1A and 1C and in clusters 6 (*S. violaceus*), 17 (*S. griseoviridis*) and 33 ('*S. chromogenus*'). To date, about a third of the strains in subcluster 1B have been lysed by phage specific for *S. griseus* (Korn *et al.*, 1978) and shown to form a distinct DNA homology group based on the *S. griseus* ISP 5326 reference system (Okanishi *et al.*, 1972). Good agreement was also found between these DNA pairing data and the numerical phenetic classification of Gyllenberg (1970). In turn, five of the species recovered in subcluster 1C (*S. olivaceus*) were listed by Hütter (1967) as synonyms of *S. olivaceus* ISP 5072. Thus, the composition and properties of *S. albidoflavus* and its subclusters are generally similar to those defined in the numerous previous studies of this important group of streptomycetes.

All of the strains in the major cluster of *S. violaceoniger* and those in seven minor clusters produced a grey spore mass. This was also true of many strains in the major clusters *S. atroolivaceus*, *S. exofoliatus*, *S. rochei*, *S. chromofuscus*, *S. cyaneus*, *S. diastaticus*, *S. olivaceoviridis*, *S. griseoruber* and *S. lydicus* (Table 9). This reflects the fact that many streptomycetes produce grey spores. It also highlights a major inadequacy of many previous artificial classifications in which spore colour was used as a major character. In contrast, few strains formed a white spore mass and most were classified in the *S. albus* cluster.

The *S. griseoruber* cluster contained four species regarded as synonyms of *S. violaceoruber* ISP 5049 (Korn *et al.*, 1978). One of these, '*S. caesius*' ISP 5419, shared a high similarity (92·8% S_{SM}) with *Actinopycnidium caeruleum* E35. The latter was recovered in a DNA homology group based on *S. violaceoruber* ISP 5049 (Monson *et al.*, 1969).

Streptomycetes producing a blue spore mass have frequently been grouped together (Hütter, 1962; Pridham & Tresner, 1974*b*; Kuryłowicz *et al.*, 1975, 1976; Korn *et al.*, 1978). Thirteen of the 19 blue-spored streptomycetes studied here were classified in *S. cyaneus* (cluster 18), which also included strains forming grey and red spores (Table 9). Many of the strains assigned to phenon 18 were also found in the blue-spored H_2 and H_3 groups of Kuryłowicz *et al.* (1975, 1976). Indeed, group H_2 was composed exclusively of blue-spored strains but, in contrast, group H_2 contained organisms allotted to nine phena in the present study. *Streptomyces*

Table 9. *Distribution of the characteristics used to delimit species-groups in Bergey's Manual of Determinative Bacteriology (Pridham & Tresner, 1974b) within the major streptomycete clusters defined at the 77·5% S_{SM} level*

Key. Spore colour: B, blue; Gn, green; Gy, grey; R, red; W, white; V, violet; Y, yellow. Spore chain morphology: RF, rectiflexibles; RA, retinaculiaperti; S, spirales. Spore surface ornamentation: Hy, hairy; Rug, rugose; Sm, smooth; Spy, spiny.

Cluster no.	Cluster name	Predominant character states: Spore colour	Spore chain morphology	Melanin pigment	Spore surface ornamentation
1	*Streptomyces albidoflavus*	Y/Gy	RF	−	Sm
3	*S. atroolivaceus*	W/Gy	RF	−	Sm
5	*S. exofoliatus*	R/Gy	RF	+/−	Sm
6	*S. violaceus*	V/Y	RF/RA/S	+	Sm/Spy
10	*S. fulvissimus*	R	RF/RA/S	+/−	Sm
12	*S. rochei*	Gy	S/RA	−	Sm/Spy/Hy
15	*S. chromofuscus*	Y/W/Gy	RF/S	+/−	Sm/Spy/Hy
16	*S. albus*	W	S	−	Sm
17	*S. griseoviridis*	R	S	−	Sm
18	*S. cyaneus*	B/R/Gy	S	+	Sm/Spy
19	*S. diastaticus*	W/R/Gy	RF/RA/S	+/−	Sm
20	*S. olivaceoviridis*	Gy	S	−	Sm
21	*S. griseoruber*	Gy	S	−	Sm
29	*S. lydicus*	Gy	S	−	Sm
32	*S. violaceoniger*	Gy	S	−	Rug/Sm
37	*S. griseoflavus*	Gn	RA	−	Spy/Hy
40	*S. phaeochromogenes*	?	RA/S	+/−	Sm
42	*S. rimosus*	W/Y	RF/S	−	Sm
61	*S. lavendulae*	R	RF	+	Sm

viridochromogenes ISP 5110 and '*S. viridis*' ISP 5381, which constituted cluster 27, also formed blue spores. In contrast to grey-spored streptomycetes, strains forming blue spores often seem to share many other characteristics.

Relatively few *Streptomyces* species form either a green or violet spore mass (Pridham & Tresner, 1974*b*). In the present investigation, '*S. cattleya*' G1 and *S. tubercidicus* ISP 5261 (cluster 47), *S. cellostaticus* ISP 5189, *S. violaceus* ISP 5082 and *S. violascens* ISP 5183 of cluster 6 (*S. violaceus*) and the single member cluster, *S. massasporeus* ISP 5035, were the only streptomycetes to form violet spores. Fifteen streptomycetes produced a green spore mass, five of which fell into the six-membered *S. griseoflavus* cluster (Table 9). The green-spored strains, therefore, formed a relatively heterogeneous group, as reported by Kuryłowicz *et al.* (1975, 1976).

Streptomyces species with red spores are relatively common and were recovered in a number of phena by Kuryłowicz *et al.* (1975, 1976). All of the strains in the *S. griseoviridis* and *S. fradiae* clusters, and many in *S. exofoliatus*, *S. fulvissimus*, *S. cyaneus*, *S. lavendulae* and *S. luridus* clusters produced red spores (Table 9).

However, only one major and nine minor clusters were homogeneous with respect to spore colour. Similarly, other pigmentation and morphological features were not taxon specific. Thus, for example, sclerotia-producing strains of *Chainia* were distributed between two major and two minor clusters. These results, together with the difficulties of determining these traditional characteristics (Shirling & Gottlieb, 1967, 1970; Szabo & Marton, 1976; Williams & Wellington, 1980), clearly show the inadequacies of classifications based on such criteria. One of these traditional characteristics, spore surface ornamentation, was of particularly limited diagnostic value. Most streptomycetes produce smooth spores and, of the major clusters, only *S. griseoflavus* and *S. violaceoniger* contained a majority of strains producing ornamented spores (Table 9). In the former, all strains produced spiny or hairy spores and in the latter, all strains had a rugose spore surface, a category recognized by Dietz & Mathews (1962, 1968, 1969, 1971) but not used in the ISP or by Pridham & Tresner (1974*b*).

The results of this study, therefore, completely vindicate the view of Sneath (1970) that numerical analysis is the only practical way of dealing with the overspeciation in the genus *Streptomyces* and that use of a few selected characters cannot reveal the natural phenetic groups within it.

CONCLUSIONS

In a study as comprehensive as this, it is appropriate to list the main implications of the results.

(1) Some rationalization of the genera within the family *Streptomycetaceae* is proposed. *Actinopycnidium*, *Actinosporangium*, *Chainia*, *Elytrosporangium* and *Microellobosporia* should be regarded as synonyms of *Streptomyces*. To accommodate these changes, the definition of the genus *Streptomyces* (see Introduction) should be extended to include species which regularly bear single or short chains of spores (1·0–3·5 μm diameter) on their substrate mycelium. *Kitasatoa* should be removed from the family *Actinoplanaceae* and also reduced to synonymy with *Streptomyces*. *Microtetraspora* should not be included in the family *Streptomycetaceae*, but is probably related to *Actinomadura*.

In addition to *Streptomyces*, the family *Streptomycetaceae* contains *Streptoverticillium*, *Nocardioides*, *Intrasporangium* and *Sporichthya* (not studied here) which show little affinity to streptomycetes and remain in the family solely on the basis of their wall chemotype I. Their taxonomic relationships will be facilitated if more strains become available.

(2) The strong phenetic relationship of *Nocardiopsis* and the weaker one of *Saccharopolyspora* to *Streptomyces* contradict the chemotaxonomic data which justify their exclusion from the family *Streptomycetaceae*.

(3) *Actinomadura sensu stricto* is phenetically, as well as chemically, distinguishable from *Streptomyces*. Likewise, '*Nocardia*' *mediterranea* can be phenetically and chemically distinguished from *Streptomyces*, *Nocardia sensu stricto* and *Actinomadura*.

(4) The S_{SM} coefficient at the 77·5% *S*-level distributed 284 streptomycete strains among 19 major clusters, 109 strains into 40 minor clusters and left 18 strains as single member clusters. The species status of the latter is clearly unaltered, but many of the minor clusters can also be regarded as species. Some of the major clusters, such as *S. albus* and *S. violaceoniger*, which were relatively small and homogeneous, could also possibly be regarded as species. Others, such as *S. albidoflavus* and *S. diastaticus*, were large and comparatively heterogeneous. Therefore, most of the major clusters should be considered as species-groups pending the results of current studies on their genetical and chemical relationships. Particular attention is being paid to the largest cluster (*S. albidoflavus*).

Therefore, over 400 *Streptomyces* species can be placed into 77 taxa of varying rank; this emphasizes the artificial nature of many previous classifications. Detailed formal proposals for any necessary nomenclatural changes will be made elsewhere.

Two of us (M.G. and S.T.W.) acknowledge support from the Science and Engineering Research Council (grants GR/A/04309, GR/A/8552). We are greatly indebted to colleagues who donated strains (Table 2), especially to Dr Akio Seino (Kaken Chemical Co. Ltd, Tokyo, Japan). The co-operation of Dr L. Nisbet and his colleagues (Glaxo Group Research, Greenford, Middlesex) is also gratefully acknowledged.

REFERENCES

AGRE, N. S., EFIMOVA, T. P. & GUZEVA, L. N. (1975). Heterogeneity of the genus *Actinomadura* Lechevalier and Lechevalier. *Mikrobiologiya* **44**, 252–257.

ALDERSON, G. & GOODFELLOW, M. (1979). Classification and identification of actinomycetes causing mycetoma. *Postepy higieny i medycyny doświadczalnej* **33**, 109–124.

ALDERSON, G., GOODFELLOW, M., WELLINGTON, E. M. H., WILLIAMS, S. T., MINNIKIN, S. M. & MINNIKIN, D. E. (1981). Chemical and numerical taxonomy of *Nocardia mediterranea*. *Zentralblatt für Bakteriologie, Mikrobiologie und Hygiene* (*I Abteilung*) Supplement **11**, 39–46.

ARAI, T. & MIKAMI, Y. (1969). Identification keys for antibiotic producing *Streptomyces*. I. Antifungal antibiotic producers. *Annual Report of the Institute of Food Microbiology, Chiba University* **22**, 59–79.

AUSTIN, B. & COLWELL, R. R. (1977). Evaluation of

some coefficients for use in numerical taxonomy of micro-organisms. *International Journal of Systematic Bacteriology* **27**, 204–210.

BALDACCI, E. (1939). Introduzione allo studio degli Attinomiceti. *Mycopathologia* **2**, 84–106.

BALDACCI, E. (1958). Development in the classification of actinomycetes. *Giornale di microbiologia* **6**, 10–27.

BALDACCI, E. & COMASCHI, G. F. (1956). Contributo alla sistematica degli attinomiceti. XVIII. *Actinomyces griseus* (Krainsky) Waksman. *Mycopathologia et mycologia applicata* **7**, 279–281.

BALDACCI, E. & LOCCI, R. (1966). A tentative arrangement of the genera in Actinomycetales. *Giornale di microbiologia* **14**, 131–139.

BALDACCI, E. & LOCCI, R. (1974). Genus II. *Streptoverticillium* Baldacci 1958, 15, emend. mut. char. Baldacci, Farina and Locci 1966, 168. In *Bergey's Manual of Determinative Bacteriology*, 8th edn, pp. 829–842. Edited by R. E. Buchanan & N. E. Gibbons. Baltimore: Williams & Wilkins.

BALDACCI, E., LOCCI, R. & LOCCI, J. R. (1966). Production of granules by Actinomycetales. *Giornale di microbiologia* **14**, 173–184.

BECKER, B., LECHEVALIER, M. P. & LECHEVALIER, H. A. (1965). Chemical composition of cell-wall preparations from strains of various form-genera of aerobic actinomycetes. *Applied Microbiology* **13**, 236–243.

BENEDICT, R. G., PRIDHAM, T. G., LINDENFELSER, L. A., HALL, H. H. & JACKSON, R. W. (1955). Further studies in the evaluation of carbohydrate utilization tests as aids in the differentiation of species of *Streptomyces*. *Applied Microbiology* **3**, 1–6.

BORDET, C., KARAHJOLI, M., GATEAU, O. & MICHEL, G. (1972). Cell walls of nocardiae and related actinomycetes; identification of the genus *Nocardia* by cell wall analysis. *International Journal of Systematic Bacteriology* **22**, 251–259.

BRADLEY, S. G. (1980). DNA reassociation and base composition. In *Microbiological Classification and Identification*, pp. 11–26. Edited by M. Goodfellow & R. G. Board. London: Academic Press.

BRADLEY, S. G. & MORDARSKI, M. (1976). Association of polydeoxyribonucleotides of deoxyribonucleic acids from nocardioform bacteria. In *The Biology of the Nocardiae*, pp. 310–336. Edited by M. Goodfellow, G. H. Brownell & J. A. Serrano. London: Academic Press.

BUCHANAN, R. E. (1918). Studies in the classification and nomenclature of the bacteria. VIII. The subgroups and genera of the Actinomycetales. *Journal of Bacteriology* **3**, 403–406.

COLLINS, M. D., PIROUZ, Y., GOODFELLOW, M. & MINNIKIN, D. E. (1977). Distribution of menaquinones in actinomycetes and corynebacteria. *Journal of General Microbiology* **100**, 221–230.

COLLINS, M. D., SHAH, H. N. & MINNIKIN, D. E. (1980). A note on the separation of natural mixtures of bacterial menaquinones using reverse phase thin-layer chromatography. *Journal of Applied Bacteriology* **48**, 277–282.

COUCH, J. N. & BLAND, C. E. (1974). *Actinoplanaceae*. In *Bergey's Manual of Determinative Bacteriology*, 8th edn. pp. 706–708. Edited by R. E. Buchanan & N. E. Gibbons. Baltimore: Williams & Wilkins.

COWAN, S. T. (1974). *Cowan and Steel's Manual for the Identification of Medical Bacteria*, 2nd edn. Cambridge: Cambridge University Press.

CROSS, T. & AL-DIWANY, J. (1981). Streptomycetes with substrate mycelium spores: the genus *Elytrosporangium*. *Zentralblatt für Bakteriologie, Mikrobiologie und Hygiene (I Abteilung)* Supplement **11**, 59–66.

CROSS, T. & GOODFELLOW, M. (1973). Taxonomy and classification of the actinomycetes. In *Actinomycetales: Characteristics and Practical Importance*, pp. 11–112. Edited by G. Sykes & F. A. Skinner, London: Academic Press.

CROSS, T., LECHEVALIER, M. P. & LECHEVALIER, H. A. (1963). A new genus of the Actinomycetales: *Microellobosporia* gen. nov. *Journal of General Microbiology* **31**, 421–429.

DIETZ, A. & MATHEWS, J. (1962). Taxonomy of carbon replication. I. An examination of *Streptomyces hygroscopicus*. *Applied Microbiology* **10**, 258–263.

DIETZ, A. & MATHEWS, J. (1968). Taxonomy of carbon replication. II. Examination of eight additional cultures of *Streptomyces hygroscopicus*. *Applied Microbiology* **16**, 935–941.

DIETZ, A. & MATHEWS, J. (1969). Scanning electron microscopy of selected members of the *Streptomyces hygroscopicus* group. *Applied Microbiology* **18**, 694–696.

DIETZ, A. & MATHEWS, J. (1971). Classification of *Streptomyces* spore surfaces into five groups. *Applied Microbiology* **21**, 527–533.

DUNPHY, P. J., PHILLIPS, P. G. & BRODIE, A. F. (1971). Separation and identification of menaquinones from microorganisms. *Journal of Lipid Research* **12**, 442–449.

ETTLINGER, L., CORBAZ, R. & HÜTTER, R. (1958). Zur Systematik der Actinomyceten. 4. Eine Arteinteilung der Gattung *Streptomyces* Waksman et Henrici. *Archiv für Mikrobiologie* **31**, 326–358.

FALCÃO DE MORAIS, J. O. (1967). The genus *Elytrosporangium* and its relationship to *Microellobosporia* and *Streptomyces*. *Hindustan Antibiotics Bulletin* **9**, 135–137.

FALCÃO DE MORAIS, J. O., BATISTA, A. C. & MASSA, D. M. G. (1966). *Elytrosporangium*: a new genus of the Actinomycetales. *Mycopathologia et mycologia applicata* **30**, 161–171.

FARINA, G. & BRADLEY, S. G. (1970). Reassociation of deoxyribonucleic acids from *Actinoplanes* and other actinomycetes. *Journal of Bacteriology* **102**, 30–35.

FLAIG, W. & KUTZNER, H. J. (1960). Beitrag zur Systematik der Gattung *Streptomyces* Waksman et Henrici. *Archiv für Mikrobiologie* **35**, 105–138.

FRAZIER, N. C. (1926). A method for the detection of changes in gelatin due to bacteria. *Journal of Infectious Diseases* **39**, 302–309.

GATTANI, M. L. (1957). Production of sclerotic granules by *Streptomyces* spp. *Nature, London* **180**, 1293–1294.

GAUSE, G. F., PREOBRAZHENSKAYA, T. P., KUDRINA, E. S., BLINOV, N. O., RYABOVA, I. D. & SVESHNIKOVA, M. A. (1957). *Problems in the Classification of Antagonistic Actinomycetes*. Moscow: State Publishing House of Medical Literature, Medzig.

GILARDI, E., HILL, L. R., TURRI, M. & SILVESTRI, L. (1960). Quantitative methods in the systematics of Actinomycetales I. *Giornale di microbiologia* **8**, 203–218.

GOODFELLOW, M. (1971). Numerical taxonomy of some norcardioform bacteria. *Journal of General Microbiology* **69**, 33–80.

GOODFELLOW, M. & ALDERSON, G. (1977). The actinomycete genus *Rhodococcus*: a home for the '*rhodochrous*' complex. *Journal of General Microbiology* **100**, 99–122.

GOODFELLOW, M. & MINNIKIN, D. E. (1977). Nocardioform bacteria. *Annual Review of Microbiology* **31**, 159–180.

GOODFELLOW, M. & MINNIKIN, D. E. (1978). Numerical and chemical methods in the classification of *Nocardia* and related taxa. *Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene* (*I Abteilung*) Supplement **6**, 43–51.

GOODFELLOW, M. & MINNIKIN, D. E. (1981). Classification of nocardioform bacteria. *Zentralblatt für Bakteriologie, Mikrobiologie und Hygiene* (*I Abteilung*) Supplement **11**, 7–16.

GOODFELLOW, M. & ORCHARD, V. A. (1974). Antibiotic sensitivity of some nocardioform bacteria and its value as a criterion for taxonomy. *Journal of General Microbiology* **83**, 375–387.

GOODFELLOW, M. & PIROUZ, T. (1982). Numerical classification of sporoactinomycetes containing *meso*-diaminopimelic acid in the cell wall. *Journal of General Microbiology* **128**, 503–527.

GOODFELLOW, M. & SCHAAL, K. P. (1979). Identification methods for *Nocardia*, *Actinomadura* and *Rhodococcus*. In *Identification Methods for Microbiologists*, 2nd edn, pp. 261–276. Edited by F. A. Skinner & D. W. Lovelock. London: Academic Press.

GOODFELLOW, M. & WAYNE, L. G. (1982). Taxonomy and nomenclature. In *Biology of the Mycobacteria*, vol. 1., pp. 472–521. Edited by C. Ratledge & J. L. Stanford. London: Academic Press.

GOODFELLOW, M., ALDERSON, G. & LACEY, J. (1979). Numerical taxonomy of *Actinomadura* and related actinomycetes. *Journal of General Microbiology* **112**, 95–111.

GOODFELLOW, M., MINNIKIN, D. E., TODD, C., ALDERSON, G., MINNIKIN, S. M. & COLLINS, M. D. (1982). Numerical and chemical classification of *Nocardia amarae*. *Journal of General Microbiology* **128**, 1283–1297.

GORDON, R. E. (1966). Some criteria for the recognition of *Nocardia madurae* (Vincent) Blanchard. *Journal of General Microbiology* **45**, 355–364.

GORDON, R. E. (1968). The taxonomy of soil bacteria. In *The Ecology of Soil Bacteria*, pp. 293–321. Edited by T. R. G. Gray & D. Parkinson. Liverpool: Liverpool University Press.

GORDON, R. E. & HORAN, A. C. (1968*a*). A piecemeal description of *Streptomyces griseus* (Krainsky) Waksman & Henrici. *Journal of General Microbiology* **50**, 223–233.

GORDON, R. E. & HORAN, A. C. (1968*b*). *Nocardia dassonvillei*, a macroscopic replica of *Streptomyces griseus*. *Journal of General Microbiology* **50**, 235–240.

GOTTLIEB, D. & SHIRLING, E. B. (1967). Cooperative description of type cultures of *Streptomyces*. I. The International *Streptomyces* Project. *International Journal of Systematic Bacteriology* **17**, 315–322.

GYLLENBERG, H. G. (1970). Factor analytical evaluation of patterns of correlated characteristics in streptomycetes. In *The Actinomycetales*, pp. 101–105. Edited by H. Prauser. Jena: Gustav Fischer Verlag.

GYLLENBERG, H. G. (1974). Identification models for streptomycetes. *Postepy higieny i medycyny doświadczalnej* **28**, 409–418.

GYLLENBERG, H. G. (1976). Application of automation to the identification of streptomycetes. In *Actinomycetes: The Boundary Microorganisms*, pp. 299–321. Edited by T. Arai. Tokyo: Toppan Co.

GYLLENBERG, H. G., WÓZNICKA, W. & KURYŁOWICZ, W. (1967). Application of factor analysis in microbiology. 3. A study of the 'yellow series' of streptomycetes. *Annales Academiae scientiarum fennicae, Series A* (*IV. Biologica*) **114**, 3–15.

GYLLENBERG, H. G., NIEMELÄ, T. K. & NIEMI. J. S. (1975). A model for automatic identification of streptomycetes. *Postepy higieny i medycyny doświadczalnej* **29**, 357–383.

HANKIN, L., ZUCKER, M. & SANDS, D. C. (1971). Improved solid medium for the detection and enumeration of pectolytic bacteria. *Applied Microbiology* **22**, 205–209.

HASEGAWA, T., LECHEVALIER, M. P. & LECHEVALIER, H. A. (1979). Phospholipid composition of motile actinomycetes. *Journal of General and Applied Microbiology* **25**, 209–213.

HILL, L. R. & SILVESTRI, L. G. (1962). Quantitative methods in the systematics of Actinomycetales. III. The taxonomic significance of physiological-biochemical characters and the construction of a diagnostic key. *Giornale di microbiologia* **10**, 1–28.

HILL, L. R., TURRI, M., GILARDI, E. & SILVESTRI, L. G. (1961). Quantitative methods in the systematics of Actinomycetales. II. *Giornale di microbiologia* **9**, 56–72.

HOLMBERG, K. & NORD, C. E. (1975). Numerical taxonomy and laboratory identification of *Actinomyces* and *Arachnia* and some related bacteria. *Journal of General Microbiology* **91**, 17–44.

HSU, S. C. & LOCKWOOD, J. L. (1975). Powdered chitin agar as a selective medium for enumeration of actinomycetes in water and soil. *Applied Microbiology* **29**, 422–426.

HÜTTER, R. (1962). Zur Systematik der Actinomyceten. 8. Quirlbildende Streptomyceten. *Archiv für Mikrobiologie* **43**, 365–391.

HÜTTER, R. (1963). Zur Systematik der Actinomyceten. 10. Streptomyceten mit griseus-Luftmycel. *Giornale di microbiologia* **11**, 191–246.

HÜTTER, R. (1965). Die Gattungen der Actinomycetales. *Pathologia et microbiologia* **28**, 567–574.

HÜTTER, R. (1967). *Systematik der Streptomyceten*. Basel: S. Karger.

HÜTTER, R. (1970). The *Streptomyces* complex. In *The Actinomycetales*, pp. 55–66. Edited by H. Prauser. Jena: Gustav Fischer Verlag.

JENSEN, H. L. (1930). Actinomycetes in Danish soils. *Soil Science* **30**, 59–77.

JENSEN, H. L. (1931). Contribution to our knowledge of the Actinomycetales. II. The definition and subdivision of the genus *Actinomyces*, with a preliminary account of Australian soil actinomycetes. *Proceedings of the Linnean Society of New South Wales* **56**, 345–370.

JONES, D. & SACKIN, M. J. (1980). Numerical methods in the classification and identification of bacteria with especial reference to the *Enterobacteriaceae*. In

Microbiological Classification and Identification, pp. 73–106. Edited by M. Goodfellow & R. G. Board. London: Academic Press.

JONES, K. L. (1949). Fresh isolates of actinomycetes in which the presence of sporogenous aerial mycelia is a fluctuating characteristic. *Journal of Bacteriology* **57**, 141–145.

KALAKOUTSKII, L. V., KIRILLOVA, I. & KRASILNIKOV, N. A. (1967). A new genus of the Actinomycetales – *Intrasporangium* gen. nov. *Journal of General Microbiology* **48**, 79–85.

KHAN, M. R. & WILLIAMS, S. T. (1975). Studies on the ecology of actinomycetes in soil. VIII. Distribution and characteristics of acidophilic actinomycetes. *Soil Biology and Biochemistry* **7**, 345–348.

KONEV, YU. E. & MITNITSKII, A. B. (1980). Numeric taxonomy of verticillate actinomycetes. *Mikrobiologiya* **49**, 110–116.

KORN, F., WEINGÄRTNER, B. & KUTZNER, H. J. (1978). A study of twenty actinophages: morphology, serology, relationship and host range. In *Genetics of the Actinomycetales*, pp. 251–270. Edited by E. Freerksen, I. Tarnok and J. H. Thumin. Stuttgart: Gustav Fischer Verlag.

KRAINSKY, A. (1914). Die Aktinomyceten und ihre Bedeutung in der Natur. *Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene* (*II Abteilung*) **41**, 649–688.

KRASILNIKOV, N. A. (1938). *Ray Fungi And Related Organisms. Actinomycetales.* Moscow: Izdatel'stvo Akademii Nauk SSSR.

KRASILNIKOV, N. A. (1962). A new genus of ray fungus – *Actinopycnidium* n. gen. of family *Actinomycetaceae. Mikrobiologiya* **31**, 204–207.

KRASILNIKOV, N. A. & YUAN, C. S. (1961). *Actinosporangium*, a new genus of the family *Actinoplanaceae. Izvestiya Akademii nauk SSR* (*Seriya biologicheskaya*) **8**, 113–116.

KROPPENSTEDT, R. M. & KUTZNER, H. J. (1976). Biochemical markers in the taxonomy of the Actinomycetales. *Experientia* **32**, 318–319.

KROPPENSTEDT, R. M. & KUTZNER, H. J. (1978). Biochemical taxonomy of some problem actinomycetes. *Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene* (*I Abteilung*) Supplement **6**, 125–133.

KROPPENSTEDT, R. M., KORN-WENDISCH, F., FOWLER, V. J. & STACKEBRANDT, E. (1981). Biochemical and molecular genetic evidence for a transfer of *Actinoplanes armeniacus* into the family *Streptomycetaceae. Zentralblatt für Bakteriologie, Mikrobiologie und Hygiene* (*I Abteilung, Originale C*) **2**, 254–262.

KURYŁOWICZ, W., WOŹNICKA, W., MALINOWSKI, K. & PASZKIEWICZ, A. (1969). Taxonomic investigation of six actinomyces series. *Experimental Medicine and Microbiology* **21**, 143–151.

KURYŁOWICZ, W., WOŹNICKA, W., PASZKIEWICZ, A. & MALINOWSKI, K. (1970). Application of numeric taxonomy in streptomycetes. In *The Actinomycetales*, pp. 107–122. Edited by H. Prauser. Jena: Gustav Fischer Verlag.

KURYŁOWICZ, W., PASZKIEWICZ, A., WOŹNICKA, W., KURZATKOWSKI, W. & SZULGA, T. (1975). Classification of *Streptomyces* by different numerical methods. *Postepy higieny i medycyny doświadczalnej* **29**, 281–355.

KURYŁOWICZ, W., PASZKIEWICZ, A., WOŹNICKA, W. & KURZATKOWSKI, W. (1976). Numerical taxonomy of streptomycetes (ISP strains). In *Actinomycetes: The Boundary Organisms*, pp. 323–340. Edited by T. Arai. Tokyo: Toppan Co.

KÜSTER, E. (1963). Morphological and physiological aspects of the taxonomy of streptomycetes. *Microbiologica española* **16**, 193–202.

KÜSTER, E. (1972). Simple working key for the classification and identification of named taxa included in the International *Streptomyces* Project. *International Journal of Systematic Bacteriology* **22**, 139–148.

KÜSTER, E. & WILLIAMS, S. T. (1964). Production of hydrogen sulphide by streptomycetes and methods for its detection. *Applied Microbiology* **12**, 46–52.

KUTZNER, H. J. (1976). *Methoden zur Untersuchung von Streptomyceten und einigen anderen Actinomyceten.* Darmstadt: Teilsammlung Darmstadt am Institut für Mikrobiologie der Technischen Hochschule.

KUTZNER, H. J. (1981). *Streptomycetaceae.* In *The Prokaryotes: A Handbook of Habitats, Isolation and Identification of Bacteria*, pp. 2028–2090. Edited by M. P. Starr, H. Stolp, H. G. Trüper, A. Balows & H. G. Schlegel. Berlin: Springer Verlag.

KUTZNER, H. J. & WAKSMAN, S. A. (1959). *Streptomyces coelicolor* Müller and *Streptomyces violaceoruber* Waksman and Curtis, two distinctly different organisms. *Journal of Bacteriology* **78**, 528–538.

KUTZNER, H. J., BÖTTIGER, V. & HEITZER, R. D. (1978). The use of physiological criteria in the taxonomy of *Streptomyces* and *Streptoverticillium. Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene* (*I Abteilung*) Supplement **6**, 25–29.

LACEY, J. & GOODFELLOW, M. (1975). A novel actinomycete from sugar-cane bagasse: *Saccharopolyspora hirsuta* gen. et sp. nov. *Journal of General Microbiology* **88**, 75–85.

LACEY, J., GOODFELLOW, M. & ALDERSON, G. (1978). The genus *Actinomadura* Lechevalier and Lechevalier. *Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene* (*I Abteilung*) Supplement **6**, 107–117.

LECHEVALIER, H. A. & LECHEVALIER, M. P. (1965). Classification des actinomycetes aérobies basée sur leur morphologie et leur composition chimique. *Annales de l'Institut Pasteur* **108**, 662–673.

LECHEVALIER, H. A. & LECHEVALIER, M. P. (1967). Biology of actinomycetes. *Annual Review of Microbiology* **21**, 71–100.

LECHEVALIER, H. A. & LECHEVALIER, M. P. (1970*a*). A critical evaluation of the genera of aerobic actinomycetes. In *The Actinomycetales*, pp. 393–405. Edited by H. Prauser. Jena: Gustav Fischer Verlag.

LECHEVALIER, H. A., LECHEVALIER, M. P. & GERBER, N. N. (1971). Chemical composition as a criterion in the classification of actinomycetes. *Advances in Applied Microbiology* **14**, 47–72.

LECHEVALIER, M. P. & GERBER, N. N. (1970). The identity of madurose with 3-*o*-methyl-D-galactose. *Carbohydrate Research* **13**, 451–454.

LECHEVALIER, M. P. & LECHEVALIER, H. A. (1970*b*). Chemical composition as a criterion in the classification of aerobic actinomycetes. *International Journal of Systematic Bacteriology* **20**, 435–443.

LECHEVALIER, M. P., LECHEVALIER, H. A. & HOLBERT, P. E. (1968). *Sporichthya*, un nouveau genre de *Streptomycetaceae*. *Annales de l'Institut Pasteur* **114**, 277–285.

LECHEVALIER, M. P., LECHEVALIER, H. A. & HEINTZ, E. E. (1973). Morphological and chemical nature of the sclerotia of *Chainia olivacea* Thirumalachar and Sukapure of the order Actinomycetales. *International Journal of Systematic Bacteriology* **23**, 157–170.

LECHEVALIER, M. P., DE BIEVRE, C. & LECHEVALIER, H. A. (1977). Chemotaxonomy of aerobic actinomycetes: phospholipid composition. *Biochemical Systematics and Ecology* **5**, 249–260.

LEDERER, E., ADAM, A., CIOBARU, R., PETIT, J.-F. & WIETZERBIN, J. (1975). Cell walls of mycobacteria and related organisms; chemistry and immunostimulant properties. *Molecular and Cellular Biochemistry* **7**, 87–104.

LIESKE, R. (1921). *Morphologie und Biologie der Strahlenpilze*. Leipzig: Bontraeger.

LOCCI, R., BALDACCI, E. & BALDAN, B. P. (1969). The genus *Streptoverticillium*. A taxonomic study. *Giornale di microbiologia* **17**, 1–60.

LYONS, A. J., JR & PRIDHAM, T. G. (1966). *Streptomyces griseus* (Krainsky) Waksman and Henrici. A taxonomic study of some strains. *Technical Bulletin, Agricultural Research Service, United States Department of Agriculture* no. 1360.

MATSUMAE, A. M. & HATA, T. (1968). A new genus of Actinomycetales: *Kitasatoa* gen. nov. *Journal of Antibiotics* **21**, 616–625.

MINNIKIN, D. E. & GOODFELLOW, M. (1976). Lipid composition in the classification and identification of nocardiae and related taxa. In *The Biology of the Nocardiae*, pp. 160–219. Edited by M. Goodfellow, G. H. Brownell & J. A. Serrano. London: Academic Press.

MINNIKIN, D. E. & GOODFELLOW, M. (1978). Polar lipids of nocardioform and related bacteria. *Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene* (*I Abteilung*) Supplement **6**, 75–83.

MINNIKIN, D. E. & GOODFELLOW, M. (1980). Lipid composition in the classification and identification of acid-fast bacteria. In *Microbiological Classification and Identification*, pp. 189–256. Edited by M. Goodfellow & R. G. Board. London: Academic Press.

MINNIKIN, D. E. & GOODFELLOW, M. (1981). Lipids in the classification of actinomycetes. *Zentralblatt für Bakteriologie, Mikrobiologie und Hygiene*. (*I Abteilung*) Supplement **11**, 99–109.

MINNIKIN, D. E., PIROUZ, T. & GOODFELLOW, M. (1977). Polar lipid composition in the classification of some *Actinomadura* species. *International Journal of Systematic Bacteriology* **27**, 118–121.

MÖLLER, F. (1962). Quantitative methods in the systematics of Actinomycetales. IV. The theory and application of a probabilistic identification key. *Giornale di microbiologia* **10**, 29–47.

MONSON, A. M., BRADLEY, S. G., ENQUIST, L. W. & CRUCES, G. (1969). Genetic homologies among *Streptomyces violaceoruber* strains. *Journal of Bacteriology* **99**, 702–706.

MORDARSKA, H., MORDARSKI, M. & GOODFELLOW, M. (1972). Chemotaxonomic characters and classification of some nocardioform bacteria. *Journal of General Microbiology* **71**, 77–86.

MORDARSKI, M., GOODFELLOW, M., TKACZ, A., PULVERER, G. & SCHAAL, K. P. (1980*a*). Ribosomal ribonucleic acid similarities in the classification of *Rhodococcus* and related taxa. *Journal of General Microbiology* **118**, 313–319.

MORDARSKI, M., GOODFELLOW, M., SZYBA, K., TKACZ, A., PULVERER, G. & SCHAAL, K. P. (1980*b*). Deoxyribonucleic acid reassociation in the classification of the genus *Rhodococcus* Zopf 1891 (Approved Lists, 1980). *International Journal of Systematic Bacteriology* **30**, 521–527.

MORDARSKI, M., KASZEN, I., TKACZ, A., GOODFELLOW, M., ALDERSON, G., SCHAAL, K. P. & PULVERER, G. (1981). Deoxyribonucleic acid pairing in the classification of the genus *Rhodococcus*. *Zentralblatt für Bakteriologie, Parasitenkunde Infektionskrankheiten und Hygiene* (*I Abteilung*) Supplement **11**, 25–31.

NITSCH, B. & KUTZNER, H. J. (1968). Ureaseaktivität bei Streptomyceten. *Zeitschrift für Naturforschung* **23b**, 565.

NITSCH, B. & KUTZNER, H. J. (1969*a*). Decomposition of oxalic acid and other organic acids by streptomycetes as a taxonomic aid. *Zeitschrift für Allgemeine Mikrobiologie* **9**, 613–632.

NITSCH, B. & KUTZNER, H. J. (1969*b*). Egg-yolk agar as a diagnostic medium for streptomycetes. *Experientia* **25**, 113.

NONOMURA, H. (1974). Key for the classification and identification of 458 species of streptomycetes included in the ISP. *Journal of Fermentation Technology* **52**, 78–92.

O'CALLAGHAN, C., MORRIS, A., KIRBY, S. M. & SHINGLER, A. H. (1972). Novel method for detection of β-lactamases by using a chromogenic cephalosporin substrate. *Antimicrobial Agents and Chemotherapy* **1**, 283–288.

OKAMI, Y. (1952). Utilization of nitrogen compounds by *Streptomycetaceae* and its application to classification. *Japanese Journal of Medical Sciences and Biology* **5**, 265–275.

OKANISHI, M. & GREGORY, K. F. (1970). Methods for the determination of deoxyribonucleic acid homologies in *Streptomyces*. *Journal of Bacteriology* **104**, 1086–1094.

OKANISHI, M., AKAGAWA, H. & UMEZAWA, H. (1972). An evaluation of taxonomic criteria in streptomycetes on the basis of deoxyribonucleic acid homology. *Journal of General Microbiology* **72**, 49–58.

ORCHARD, V. A. & GOODFELLOW, M. (1980). Numerical classification of some named strains of *Nocardia asteroides* and related isolates from soil. *Journal of General Microbiology* **118**, 295–312.

ØRSKOV, J. (1923). *Investigations into the Morphology of the Ray Fungi*. Copenhagen: Levin & Munksgaard.

PASZKIEWICZ, A. (1972). Application of numerical methods to the taxonomy of the genus *Streptomyces*. *Archivum immunologiae et therapiae experimentalis* **20**, 307–332.

PIOT, P., VAN DYCK, E., GOODFELLOW, M. & FALKOW, S. (1980). A taxonomic study of *Gardnerella vaginalis* (*Haemophilus vaginalis*) Gardner and Dukes 1955. *Journal of General Microbiology* **119**, 373–396.

POMMIER, M. T. & MICHEL, G. (1973). Phospholipid

and acid composition of *Nocardia* and nocardoid bacteria as criteria of classification. *Biochemical Systematics* **1**, 3–12.

PRAUSER, H. (1970). Characters and genera arrangement in the Actinomycetales. In *The Actinomycetales*, pp. 407–418. Edited by H. Prauser. Jena: Gustav Fischer Verlag.

PRAUSER, H. (1976*a*). *Nocardioides*, a new genus of the order Actinomycetales. *International Journal of Systematic Bacteriology* **26**, 58–65.

PRAUSER, H. (1976*b*). Host–phage relationships in nocardioform organisms. In *The Actinomycetales*, pp. 266–284. Edited by M. Goodfellow, G. H. Brownell & J. A. Serrano. London: Academic Press.

PRAUSER, H. (1978). Considerations on taxonomic relations among Gram-positive, branching bacteria. *Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene* (*I Abteilung*) Supplement **6**, 3–12.

PRAUSER, H. & BERGHOLZ, M. (1974). Taxonomy of actinomycetes and screening for antibiotic substances. *Postepy higieny i medycyny doświadczalnej* **28**, 441–457.

PRAUSER, H. & FALTA, R. (1968). Phagensensibilität, Zellwand-Zusammensetzung und Taxonomie von Actinomyceten. *Zeitschrift für Allgemeine Mikrobiologie* **8**, 39–46.

PRAUSER, H., MÜLLER, L. & FALTA, R. (1967). On the taxonomic position of the genus *Microellobosporia* Cross, Lechevalier & Lechevalier 1961. *International Journal of Systematic Bacteriology* **17**, 361–366.

PRIDHAM, T. G. (1963–1964). Taxonomic studies of *Streptomyces griseus* (*Krainsky*) Waksman et Henrici: a species comprising many subspecies. *Antimicrobial Agents and Chemotherapy* **1963–1964**, 104–115.

PRIDHAM, T. G. (1970). New names and combinations in the order Actinomycetales Buchanan 1917. *Technical Bulletin, Agricultural Research Service, United States Department of Agriculture* no. 1424.

PRIDHAM, T. G. (1976). Contemporary species concepts in Actinomycetales. In *Actinomycetes: The Boundary Microorganisms*, pp. 163–174. Edited by T. Arai. Tokyo: Toppan Co.

PRIDHAM, T. G. & GOTTLIEB, D. (1948). The utilization of carbon compounds by some Actinomycetales as an aid for species determination. *Journal of Bacteriology* **56**, 107–114.

PRIDHAM, T. G. & LYONS, JR, A. J. (1969). Progress in the clarification of the taxonomic and nomenclatural status of some problem actinomycetes. *Developments in Industrial Microbiology* **10**, 183–221.

PRIDHAM, T. G. & TRESNER, H. D. (1974*a*). Family VII. *Streptomycetaceae* Waksman and Henrici 1943, 339. In *Bergey's Manual of Determinative Bacteriology*, 8th edn, pp. 747–748. Edited by R. E. Buchanan & N. E. Gibbons. Baltimore: Williams & Wilkins.

PRIDHAM, T. G. & TRESNER, H. D. (1974*b*). *Streptomyces* Waksman and Henrici 1943, 339. In *Bergey's Manual of Determinative Bacteriology*, 8th edn, pp. 748–829. Edited by R. E. Buchanan & N. E. Gibbons. Baltimore: Williams & Wilkins.

PRIDHAM, T. G., ANDERSON, P., FOLEY, C., LINDENFELSER, H. A., HESSELTINE, C. W. & BENEDICT, R. G. (1956–1957). A selection of media for maintenance and taxonomic study of *Streptomyces*. *Antibiotics Annual* **1956–1957**, 947–953.

PRIDHAM, T. G., HESSELTINE, C. W. & BENEDICT, R. G. (1958). A guide for the classification of streptomycetes according to selected groups. Placement of strains in morphological sections. *Applied Microbiology* **6**, 52–79.

PRIDHAM, T. G., LYONS, A. J. & SECKINGER, H. L. (1965). Comparison of some dried holotype and neotype specimens with their living counterparts. *International Bulletin of Bacteriological Nomenclature and Taxonomy* **15**, 191–237.

RANCOURT, M. & LECHEVALIER, H. A. (1963). Electron microscopic observation of the sporangial structure of an actinomycete: *Microellobosporia flavea*. *Journal of General Microbiology* **31**, 495–498.

SCHOFIELD, G. M. & SCHAAL, K. P. (1981). A numerical taxonomic study of members of the *Actinomycetaceae* and related taxa. *Journal of General Microbiology* **127**, 237–259.

SHIBATA, M. HASEGAWA, T. & HIGASHIDE, E. (1971). Tolypomycin, a new antibiotic. I. *Streptomyces tolypophorus* nov. sp., a new antibiotic, tolypomycin-producer. *Journal of Antibiotics* **24**, 810–816.

SHINOBU, R. (1958). Physiological and cultural study for the identification of soil actinomycetes species. *Memoirs of the Osaka University of the Liberal Arts and Education* (*B. Natural Science*), **7**, 1–76.

SHIRLING, E. B. & GOTTLIEB, D. (1966). Methods for characterisation of *Streptomyces* species. *International Journal of Systematic Bacteriology* **16**, 313–340.

SHIRLING, E. B. & GOTTLIEB, D. (1968*a*). Cooperative description of type cultures of *Streptomyces*. II. Species descriptions from first study. *International Journal of Systematic Bacteriology* **18**, 69–189.

SHIRLING, E. B. & GOTTLIEB, D. (1968*b*). Cooperative description of type cultures of *Streptomyces*. III. Additional species descriptions from first and second studies. *International Journal of Systematic Bacteriology* **18**, 279–391.

SHIRLING, E. B. & GOTTLIEB, D. (1969). Cooperative description of type cultures of *Streptomyces*. IV. Species descriptions from the second, third and fourth studies. *International Journal of Systematic Bacteriology* **19**, 391–512.

SHIRLING, E. B. & GOTTLIEB, D. (1972). Cooperative description of type strains of *Streptomyces*. V. Additional descriptions. *International Journal of Systematic Bacteriology* **22**, 265–394.

SHIRLING, E. B. & GOTTLIEB, D. (1976). Retrospective evaluation of International *Streptomyces* Project special criteria. In *Actinomycetes: The Boundary Microorganisms*, pp. 9–41. Edited by T. Arai. Tokyo: Toppan Co.

SIERRA, G. (1957). A simple method for the detection of lipolytic activity of microorganisms and some observations on the influence of the contact between cells and fatty substrates. *Antonie van Leeuwenhoek* **23**, 15–22.

SILVESTRI, L. G., TURRI, M., HILL., L. R. & GILARDI, E. (1962). A quantitative approach to the systematics of actinomycetes based on overall similarity. *Symposia of the Society for General Microbiology* **12**, 333–360.

SKERMAN, V. B. D., MCGOWAN, V. & SNEATH, P. H. A.

(1980). Approved lists of bacterial names. *International Journal of Systematic Bacteriology* **30**, 225–420.

SNEATH, P. H. A. (1957). The application of computers to taxonomy. *Journal of General Microbiology* **17**, 201–226.

SNEATH, P. H. A. (1970). Application of numerical taxonomy to Actinomycetales: Problems and perspectives. In *The Actinomycetales* pp. 371–378. Edited by H. Prauser. Jena: Gustav Fischer Verlag.

SNEATH, P. H. A. (1976). An evaluation of numerical taxonomic techniques in the taxonomy of *Nocardia* and allied taxa. In *The Biology of the Nocardiae*, pp. 74–101. Edited by M. Goodfellow, G. H. Brownell & J. A. Serrano. London: Academic Press.

SNEATH, P. H. A. (1977). A method for testing the distinctness of clusters: a test of the disjunction of two clusters in Euclidean space as measured by their overlap. *Journal of Mathematical Geology* **9**, 123–143.

SNEATH, P. H. A. (1979). Basic program for a significance test for two clusters in Euclidean space as measured by their overlap. *Computers & Geosciences* **5**, 143–155.

SNEATH, P. H. A. & JOHNSON, R. (1972). The influence on numerical taxonomic similarities of errors in microbiological tests. *Journal of General Microbiology* **72**, 377–392.

SNEATH, P. H. A. & SOKAL, R. R. (1973). *Numerical Taxonomy. The Principles and Practice of Numerical Classification.* San Francisco: W. H. Freeman.

SNEATH, P. H. A. & STEVENS, M. (1967). A divided Petri dish for use with multipoint inoculators. *Journal of Applied Bacteriology* **30**, 495–497.

SOKAL, R. R. & MICHENER, C. D. (1958). A statistical method for evaluating systematic relationships. *Kansas University Science Bulletin* **38**, 1409–1438.

STACKEBRANDT, E. & WOESE, C. R. (1981). The evolution of prokaryotes. *Symposia of the Society for General Microbiology* **32**, 1–31.

STACKEBRANDT, E., WUNNER-FÜSSL, B., FOWLER, V. J. & SCHLEIFER, K-H. (1981). Deoxyribonucleic acid homologies and ribosomal ribonucleic acid similarities among sporeforming members of the order Actinomycetales. *International Journal of Systematic Bacteriology* **31**, 420–431.

SZABO, I. M. & MARTON, M. (1976). Evaluation of criteria used in the ISP cooperative description of type strains of *Streptomyces* and *Streptoverticillium* species. *International Journal of Systematic Bacteriology* **26**, 105–110.

SZABO, I. M., MARTON, M., BUTI, I. & FERNANDEZ, C. (1975). A diagnostic key for the identification of 'species' of *Streptomyces* and *Streptoverticillium* included in the International *Streptomyces* Project. *Acta botanica Academiae scientiarum hungaricae* **21**, 387–418.

SZULGA, T. (1978). A critical evaluation of taxonomic procedures applied to *Streptomyces*. *Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene* (*I Abteilung*) Supplement **6**, 31–42.

TEWFIK, E. M. & BRADLEY, S. G. (1967). Characterization of deoxyribonucleic acids from streptomycetes and nocardiae. *Journal of Bacteriology* **94**, 1994–2000.

THIEMANN, J. E., PAGANI, H. & BERETTA, G. (1968). A new genus of the Actinomycetales: *Microtetraspora* gen. nov. *Journal of General Microbiology* **50**, 295–303.

THIEMANN, J. E., ZUCCO, G. & PELIZZA, G. (1969). A proposal for the transfer of *Streptomyces mediterranei* Margalith and Beretta 1960 to the genus *Nocardia* as *Nocardia mediterranea* (Margalith and Beretta) comb. nov. *Archiv für Mikrobiologie* **67**, 147–155.

THIRSK, M. L. (1957). Hippurate hydrolysis in *Klebsiella–Cloaca* classification. *Journal of General Microbiology* **17**, 390–395.

THIRUMALACHAR, M. J. (1955). *Chainia*, a new genus of the Actinomycetales. *Nature, London* **176**, 934–935.

TILLE, D., PRAUSER, H., SZYBA, K. & MORDARSKI, M. (1978). On the taxonomic position of *Nocardioides albus* Prauser by DNA:DNA-hybridization. *Zeitschrift für allgemeine Mikrobiologie* **18**, 459–462.

TOYAMA, H., OKANISHI, M. & UMEZAWA, H. (1974). Heterogeneity among whorl-forming streptomycetes determined by DNA reassociation. *Journal of General Microbiology* **80**, 507–514.

TREJO, W. H. (1970). An evaluation of some concepts and criteria used in the speciation of streptomycetes. *Transactions of the New York Academy of Sciences* **32**, 989–997.

TRESNER, H. D. & BACKUS, E. J. (1963). System of color wheels for streptomycete taxonomy. *Applied Microbiology* **11**, 335–338.

TRESNER, H. D. & DANGA, F. (1958). Hydrogen sulphide production by *Streptomyces* as a criterion for species differentiation. *Journal of Bacteriology* **76**, 239–244.

TRESNER, H. D., DAVIES, M. C. & BACKUS, E. J. (1961). Electron microscopy of *Streptomyces* spore morphology and its role in species differentiation. *Journal of Bacteriology* **81**, 70–80.

TRESNER, H. D., HAYES, J. A. & BACKUS, E. J. (1968). Differential tolerance of streptomycetes to sodium chloride as a taxonomic aid. *Applied Microbiology* **16**, 1134–1136.

TSUKAMURA, M. (1969). Numerical taxonomy of the genus *Nocardia*. *Journal of General Microbiology* **56**, 265–287.

TSYGANOV, V. A., NAMESTNIKOVA, V. P. & KRASSIKOVA, W. V. (1966). DNA composition in various mycobacteria. *Journal of Bacteriology* **96**, 1915–1919.

WAKSMAN, S. A. (1919). Cultural studies of species of *Actinomyces*. *Soil Science* **8**, 71–215.

WAKSMAN, S. A. (1940). On the classification of actinomycetes. *Journal of Bacteriology* **39**, 549–558.

WAKSMAN, S. A. (1957). Species concept among the actinomycetes with special reference to the genus *Streptomyces*. *Bacteriological Reviews* **21**, 1–29.

WAKSMAN, S. A. (1959). Strain specificity and production of antibiotic substances. X. Characterisation and classification of species within the *S. griseus* group. *Proceedings of the National Academy of Sciences of the United States of America* **45**, 1043–1047.

WAKSMAN, S. A. (1961). *The Actinomycetes*, vol. II. Baltimore: Williams & Wilkins.

WAKSMAN, S. A. & CURTIS, R. E. (1916). The actinomyces of the soil. *Soil Science* **1**, 99–134.

WAKSMAN, S. A. & HENRICI, A. T. (1943). The nomenclature and classification of the actinomycetes. *Journal of Bacteriology* **46**, 337–341.

WELLINGTON, E. M. H. & WILLIAMS, S. T. (1978). Preservation of actinomycete inoculum in frozen glycerol. *Microbios Letters* **6**, 151–157.

WELLINGTON, E. M. H. & WILLIAMS, S. T. (1981). Host ranges of phage isolated to *Streptomyces* and other genera. *Zentralblatt für Bakteriologie, Mikrobiologie und Hygiene* (*I Abteilung*) Supplement **11**, 93–98.

WILLIAMS, S. T. (1967). Sensitivity of streptomycetes to antibiotics as a taxonomic character. *Journal of General Microbiology* **46**, 151–160.

WILLIAMS, S. T. & DAVIES, F. L. (1967). Use of a scanning electron microscope for the examination of actinomycetes. *Journal of General Microbiology* **48**, 171–177.

WILLIAMS, S. T. & KHAN, M. R. (1974). Antibiotics – a soil microbiologist's view-point. *Postepy higieny i medycyny doświadczalnej* **28**, 395–408.

WILLIAMS, S. T. & WELLINGTON, E. M. H. (1980). Micromorphology and fine structure of actinomycetes. In *Microbiological Classification and Identification*, pp. 139–165. Edited by M. Goodfellow & R. G. Board. London: Academic Press.

WILLIAMS, S. T., DAVIES, F. L. & HALL, D. M. (1968). A practical approach to the taxonomy of actinomycetes isolated from soil. In *The Soil Ecosystem*, pp. 107–117. Edited by J. G. Sheals. Systematics Association Publication no. 8.

WILLIAMS, S. T., SHARPLES, G. P., SERRANO, J. A., SERRANO, A. A. & LACEY, J. (1976). The micromorphology and fine structure of nocardioform organisms. In *The Biology of the Nocardiae*, pp. 102–140. Edited by M. Goodfellow, G. H. Brownell & J. A. Serrano. London: Academic Press.

WILLIAMS, S. T., WELLINGTON, E. M. H., GOODFELLOW, M., ALDERSON, G., SACKIN, M. & SNEATH, P. H. A. (1981). The genus *Streptomyces* – a taxonomic enigma. *Zentralblatt für Bakteriologie, Mikrobiologie und Hygiene* (*I Abteilung*) Supplement **11**, 47–58.

WILLIAMS, S. T., GOODFELLOW, M., WELLINGTON, E. M. H., VICKERS, J. C., ALDERSON, G., SNEATH, P. H. A., SACKIN, M. J. & MORTIMER, A. M. (1983). A probability matrix for identification of some streptomycetes. *Journal of General Microbiology* **129**, 1815–1830.

WISHART, D. (1978). *Clustan User Manual. Version 1C, Release 2*, 3rd edn. Edinburgh: Edinburgh University Program Library Unit.

WÓZNICKA, W. (1965). *Taxonomic and Taxonometric Studies on 'Yellow Series' of Actinomycetes*. Warsaw: Panstowowz Zakad Higieny.

WÓZNICKA, W. (1967). Trials of classification of the 'yellow series' of actinomycetes. II. Taxometric studies. *Experimental Medicine and Microbiology* **21**, 143–151.

YAMADA, Y., YAMASHITA, M., TAHARA, Y. & KONDO, K. (1977). The menaquinone system in the classification of the genus *Actinomadura*. *Journal of General and Applied Microbiology* **23**, 331–335.

YAMAGUCHI, T. (1967). Similarity in DNA of various morphologically distinct actinomycetes. *The Journal of General and Applied Microbiology* **13**, 63–71.

ZIEGLER, P. & KUTZNER, H. J. (1973). Hippurate hydrolysis as a taxonomic criterion in the genus *Streptomyces* (Order Actinomycetales). *Zeitschrift für Allgemeine Mikrobiologie* **13**, 263–270.